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ESTIMATION OF (CO)VARIANCE COMPONENTS BY WEIGHTED AND
UNWEIGHTED SYMMETRIC DIFFERENCES SQUARED, AND SELECTED
MIVQUE'S: RELATIONSHIPS BETWEEN METHODS AND RELATIVE
EFFICIENCIES

The Ohio State University

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ESTIMATION OF (CO)VARIANCE COMPONENTS BY WEIGHTED AND UNWEIGHTED
SYMMETRIC DIFFERENCES SQUARED, AND SELECTED MIVQUE'S: RELATIONSHIPS
BETWEEN METHODS AND RELATIVE EFFICIENCIES

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

John William Keele, B.S., M.S.

* * * * *

The Ohio State University

1986

Dissertation Committee:

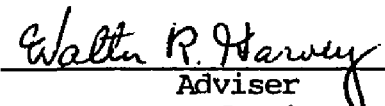
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INTRODUCTION

Variance and covariance components and ratios of these are used to characterize the type and quantity of genetic and environmental variation present in a population of animals. In addition to being unbiased and efficient (small sampling variance), it is desirable that estimates of (co)variance components be computable with a reasonable amount of computer time and memory. Even though the amount of computer time and memory considered to be reasonable has increased with improved technology, computational feasibility is still an important attribute of variance component estimation in light of the large amount of data usually needed to obtain relatively precise estimates. The challenge is to choose from the computable unbiased methods, the most efficient method.

The computational requirements for estimating genetic variance components also depend on the type of family structures that are present in the population. Populations of farm animals usually contain many different types of relatives. One way to account for relationships among animals is to use an animal model. In general, analysis of variance (ANOVA) procedures are not adequate under the animal model, although they have been used as ad hoc procedures in the past (Dickerson, 1942; Hazel et al., 1943; Eisen, 1967).

Henderson (1985a and 1985b) showed how to obtain estimates of additive and nonadditive genetic variance components by minimum

variance quadratic unbiased estimates (MIVQUE) (Rao, 1971) for assumed prior values, and restricted maximum likelihood estimates (REML) (Patterson and Thompson, 1981), under the animal model. Henderson's approach for obtaining MIVQUE and REML require the inverse of one matrix of order n and the g -inverse of another matrix of order $n+p$, where n is the number of observations, and p is the number of fixed effects. REML can be obtained by iterative MIVQUE, or by the expectation maximization (EM) algorithm (Dempster et al., 1977). Both MIVQUE and REML are not computationally feasible for large (greater than 500-1000 animals) data sets under the animal model.

When the genetic model is additive, the computational requirements for REML and MIVQUE can be reduced considerably. With the Henderson approach to obtaining MIVQUE and REML, the mixed model equations (MME) (Henderson et al., 1959) and best linear unbiased predictions of random effects (BLUP) are obtained as intermediate results. Quaas and Pollack (1980) showed that a reduced animal model (RAM) with MME only for parents of progeny with records was equivalent to the full animal model with MME for every animal. Quaas and Pollack (1980) described RAM for a multitrait model appropriate for beef cattle, and Henderson (1985c) described RAM for the unitrait case. Hudson and Kennedy (1985) were able to obtain BLUP for parents and nonparents under RAM on swine data. In this data set, there were 5.6 times as many animals as there were parents with progeny records. Therefore, using RAM instead of the animal model saves computer storage because fewer MME are needed. However, even under RAM, the number of MME probably were too large to obtain MIVQUE or REML estimates of variance components because Kennedy

et al. (1985) used a simplified model for data in which the animal model was appropriate. For the swine data set of Hudson and Kennedy (1985), there were 4,000 to 20,000 MME under RAM for the four breeds considered. A need exists for relatively efficient variance component estimation procedures that can be computed under RAM, or the animal model if there are nonadditive genetic effects for large data sets.

Henderson (1985a) suggested an approximate MIVQUE called diagonal MIVQUE or Henderson's Simple Method for data sets in which the g -inverse of the left hand side of MME is too large to compute. The relative efficiency of this method has not been well characterized under the animal model, but Henderson (cited by Hudson and Van Vleck, 1982) found this method to be more efficient than method 3 of Henderson for selected data sets in which method 3 could be used.

Another method of reducing the computations is to assume that all variances except the error variance are zero prior to applying MIVQUE (Rao, 1971). These estimates are MIVQUE if unknown variances except the error variance actually are near zero. This method is known as MIVQUE(0). However, MIVQUE(0) was found to be inefficient relative to ANOVA when the variances other than error variance were larger than the error variance for selected 2 stage nested designs (Brocklebank and Giesbrecht, 1984).

Grimes and Harvey (1980) extended the symmetric sums of products (SSP) method of Koch (1968) to the animal model. They used their method, which they called symmetric differences squared (SDS) to estimate genetic and environmental (co)variance components for weight and gain traits of 1,780 mice. While this method required little

computer storage, it required a large amount of computer time.

Christian (1980) showed how to reduce the computer time needed to perform SDS by grouping SDS resulting from pairs of individuals with the same relationship before obtaining expectations. In addition, Christian (1980) suggested that SDS could be corrected for inadmissibility (uniformly less efficient than some other method) by weighting SDS by the inverse of the error variance-covariance matrix among SDS (WSDS). However, completing the analysis by WSDS as described by Christian would require computational steps proportional to n raised to a power of four, where n is the number of observations.

Setting some of the parameters other than the error variance to zero prior to applying MIVQUE can result in a method that is less computationally demanding than MIVQUE. For example, when permanent maternal environmental effects are important, the permanent maternal environmental and residual variance could be set to nonzero priors and all other (co)variances set to zero. This method might have a higher efficiency than MIVQUE(0), without greatly increasing the computational requirements over that of MIVQUE(0). This method will be referred to in this paper as MIVQUE(0,M,E).

In addition to reducing computational requirements of variance component estimation methods, it is convenient to avoid the assignment of prior values. Rao (1971) suggested that all priors be given a value of one when nothing is known *a priori* about the (co)variance components. This method will be referred to in this paper as MIVQUE(1).

The objectives of this study are to: 1) demonstrate that SDS weighted by the inverse of the error variance-covariance matrix among SDS (WSDS) is equivalent to MIVQUE(0); 2) demonstrate that SDS weighted by the inverse of the total variance-covariance matrix among SDS is MIVQUE when the priors are correct; 3) present a computationally feasible algorithm for obtaining WSDS; and 4) evaluate the influence of the unknown parameters on the efficiency of SDS, WSDS, MIVQUE(0,M,E), and MIVQUE(1) relative to MIVQUE.

REVIEW OF LITERATURE

VARIANCE COMPONENT ESTIMATION PROBLEM

Methods of estimating genetic and environmental (co)variance components utilize records and the relationships among individuals who produced the records. Farm populations have a family structure that consists of many different types of relatives. One way to account for these relationships when estimating (co)variance components is to use the animal model (Henderson and Quaas, 1976; Quaas and Pollack, 1980; Henderson, 1985a,b,c,; Hudson and Kennedy, 1985). Analysis of variance (ANOVA) procedures are not appropriate under the animal model because the random part of the model can not be written as the sum of sets of mutually uncorrelated random effects. When the animal model is appropriate, ANOVA procedures should be weighted by the inverse of the variance-covariance matrix among the estimated covariances among relatives to be efficient (Eisen, 1967). This method is usually not computationally feasible. The methods that can be used to estimate (co)variance components assuming an animal model are (i) minimum variance quadratic unbiased estimation (MIVQUE) (Rao, 1971); (ii) maximum likelihood (ML) (Hartley and Rao, 1967); (iii) restricted maximum likelihood (REML) (Patterson and Thompson, 1971); (iv) symmetric differences squared (SDS) (Grimes and Harvey, 1980); and (v) weighted symmetric differences squared (WSDS) (Christian, 1980). In addition, various methods which are adaptations of MIVQUE (Henderson,

1984, 1985a) can be applied to an animal model.

MIVQUE AND REML FOR ANIMAL MODEL

Henderson (1985a, b) showed how to obtain MIVQUE and REML estimates of additive and nonadditive genetic variance components under an animal model. Henderson first obtained best linear unbiased predictions (BLUP) for total genotypic merits (\hat{m}) and residuals (\hat{e}), then expressed the quadratics needed for MIVQUE and REML as quadratic functions of \hat{m} and \hat{e} . This process avoids the need to obtain the inverse of the $n \times n$ variance-covariance matrix among the observations (V) where n is the number of observations. However, the inverse of the variance-covariance matrix (M) among \hat{m} is still needed to set up the mixed model equations (MME) of Henderson et al. (1959). In general, the inverse of M will be as difficult to obtain as the inverse of V when there is one record per animal. Once the MME are obtained, \hat{m} can be calculated by iteration without finding the g-inverse of C , where C is the left hand side of MME. Submatrices of the g-inverse of C are needed however to find the expectations of the quadratics in \hat{m} and \hat{e} . The quadratics in \hat{m} and \hat{e} are set equal to their expectations and the resulting equations are solved to obtain MIVQUE. Computing the g-inverse of C is costly because this matrix is of order $n+p$, where p is the number of fixed constants in the model.

In practice, the parameters are not known; therefore guesses or estimates by other methods serve as priors for the MIVQUE algorithm. The closer the priors are to the true parameters the closer the estimates will be to MIVQUE. However, the closeness of the priors to the true parameters is unknown with experimental data.

REML can be obtained by iterative MIVQUE when only estimates in the parameter space are allowed. The solution from the k^{th} iterate of iterative MIVQUE is obtained by applying MIVQUE using as priors the solution from the $(k-1)^{\text{th}}$ iterate. This process is continued until prespecified convergence criteria are met. Estimates from the literature, ANOVA estimates, MIVQUE(0) estimates, MIVQUE(1) estimates, or guesses can be used as priors for the first iterate.

REML can also be obtained by applying an expectation maximization (EM) (Dempster et al., 1977) algorithm. The EM algorithm results in much simpler calculations at each iterate of REML than iterative MIVQUE. The quadratics in \hat{m} and \hat{e} are equated to their expectations under the pretext that the prior (co)variances are correct.

Advantages of the EM algorithm are that if prior values are assigned from within the parameter space, estimates will not converge outside the parameter space, and at each iterate the likelihood is guaranteed to increase. A disadvantage of the EM algorithm is that it converges very slowly. This can be a real problem if each iterate requires 20 minutes to an hour of computer time. Iterative MIVQUE converges more rapidly than EM, however, estimates outside the parameter space occur, and computational requirements per iterate can be much greater than EM algorithm. If the computational requirements of an iterate of iterative MIVQUE are not too much greater than that of an iterate of the EM algorithm, it is this author's opinion that iterative MIVQUE should be the method chosen because iterative MIVQUE usually converges in 3 to 5 iterations whereas the EM algorithm can take well over 50 iterations to converge.

Swallow and Monahan (1984) compared MIVQUE with ANOVA estimates used as priors (MIVQUE(A)) to REML by iterative MIVQUE for 10 different number patterns for a random one-way classification using simulation. They found that the efficiencies of MIVQUE(A) and REML were of such a similar magnitude that the extra iterations required to complete REML for convergence were not justified.

NONADDITIVE RELATIONSHIP MATRICES

Henderson (1985a) showed how the matrices of coefficients of relationship for dominance (D), additive by additive epistasis (AA), additive by dominance epistasis (AD), etc. could be obtained from Wright's numerator relationship matrix (A) using results due to Cockerham (1954) when no inbreeding has occurred. When inbreeding has occurred, the nonadditive genetic effects are difficult to interpret (Cockerham, 1954); therefore an additive genetic model is usually assumed as an approximation when inbreeding exists. When an additive genetic model is assumed, the computational requirements of MIVQUE or REML can be reduced. The greatest reduction comes about because of the structure of the inverse of A, and because the inverse of A can be obtained directly without first finding A (Henderson, 1973; Quaas, 1976).

REDUCED ANIMAL MODEL

Quaas and Pollack (1980) showed that a reduced animal model (RAM) with equations in the MME only for parents who have progeny records is equivalent to a full animal model with equations in the MME for all animals. Nonparent BLUPs can be obtained from the BLUPs of their parents, the herd-year-season effects, and the residuals. Their model

was a multiple trait model which included both direct and maternal genetic effects and a correlation between direct and maternal genetic effects. Henderson (1985c) described the RAM for single traits. Utilizing RAM greatly reduces the size of the MME which reduces the computer storage required to obtain BLUP. For example, Hudson and Kennedy (1985) obtained BLUP's for swine using Ontario Record of Performance data of Yorkshire, Landrace, Hampshire, and Duroc breeds. In this data set, there were 5.6 times as many total animals as there were parents and ancestors with progeny with records. However, the computation of MIVQUE or REML estimates of (co)variance components using quadratics in BLUP still is not feasible because the g-inverse of the left-hand side of the MME is needed for these calculations; and this matrix can be quite large even under RAM.

In practice, BLUP's are computed by substituting estimates of variance components for the corresponding parameters in the MME. These estimates can come from either the same data set or from an independent data set. When estimates of variance components are used in the MME in place of true parameters, the resulting estimates of genetic values are not actually BLUP but are probably close approximations if the estimates of variance components are precise. Also, if the estimates of variance components used with BLUP are obtained from the same data set as BLUP then the BLUP estimates obtained are biased, but this bias is likely to be very slight if the data set is large.

FEASIBILITY OF REDUCED ANIMAL MODEL

Kennedy et al. (1985) estimated the variance components used by Hudson and Kennedy (1985) using an approximate REML procedure

originally due to Henderson (cited by Hudson and Van Vleck, 1982). Kennedy et al. (1985) used the same, or some of the same, data to estimate variance components as Hudson and Kennedy (1985) used to obtain BLUP. Kennedy et al. (1985) used a model in which the random effects were sires and litters. The sires and litters were assumed to have constant variances, and the correlations among sires, among litters, and between sires and litters were assumed to be zero. If RAM was appropriate for obtaining BLUP, why did these authors not use RAM to estimate variance components? The answer is that it is not feasible to use REML or MIVQUE to obtain estimates of variance components under RAM when the MME contain 4,000 to 20,000 equations as was the case in these studies. It is not known whether it is better to use an approximate genetic model and an efficient method such as REML as was done in this study, or to use a more accurate genetic model such as RAM and a less efficient method such as diagonal MIVQUE, SDS, or WSDS when the more efficient method cannot feasibly be used with RAM. In the remainder of this paper, it will be assumed the animal model or RAM is appropriate, and methods that are more computationally feasible than REML or MIVQUE will be discussed.

METHODS MORE FEASIBLE THAN MIVQUE AND REML

Henderson (1985a) proposed a method called diagonal MIVQUE when the number of MME is too large to feasibly obtain the g-inverse of the coefficient matrix (left hand side of MME). For this method, approximate solutions for genetic random effects (g) are obtained by dividing the right hand sides of MME by the corresponding diagonal element of the coefficient matrix. Quadratics in terms of approximate

g (i.e., (\hat{g})) and approximate e (i.e., (\hat{e})) are then computed. These quadratics are then equated to their expectations, and the resulting equations are solved for estimates of variance components. The expectations of these quadratics are easier to compute than expectations of quadratics in BLUP for g and e because the inverse of the diagonal elements of the coefficient matrix are used in place of the g -inverse of the coefficient matrix.

The inverse of V is proportional to I_n for most models if all variances and covariances except the residual variance are assumed to be zero for the purpose of simplifying calculations. If MIVQUE is applied in this case the resulting estimates are MIVQUE if all (co)variances except the error variance are close to zero relative to the error variance. This method was suggested by Rao (1971) to help improve computational feasibility. However, these estimates have been shown to be poor relative to ANOVA when variances other than the error variance are as large as eight times the size of the error variance for some hierarchical designs (Brockelbank and Giesbrecht, 1985). The extent to which this is true for the animal model is not known.

Grimes and Harvey (1980) extended the use of symmetric sums of products (SSP) of Koch (1967, 1968) to the animal model. They called their method symmetric differences squared (SDS). They compared the standard errors of SDS and ANOVA for a random paternal half sib analysis using simulated data and found that SDS was slightly less efficient than ANOVA for this case. Grimes and Harvey (1980) also used simulation of a maternal effects model to evaluate the standard errors of SDS estimates of variances due to direct genic effects,

maternal genic effects, permanent maternal environmental effects, and residual effects, and the covariance between direct and maternal genic effects computed from data simulated using mating designs A and B described by Thompson (1976). They found that the standard errors of the estimates were quite large even for data sets of 1,600 animals resulting from simulating 200 A or B sets. Grimes and Harvey (1980) demonstrated the computational feasibility of SDS by using it to estimate the same (co)variances as in their maternal effects simulation described above from the weight and gain traits of 1,780 mice in a random mating control population. This procedure required very little computer storage but used considerable computer time because of the calculation of 1,583,310 symmetric differences squared and their expectations.

Christian (1980) showed how the computer time requirements of SDS can be reduced by summing groups of symmetric differences squared that have the same expectation and then computing the expectation of the sum of each group of SDS. These sums and their expectations are equated, and the resulting equations solved to obtain estimates of (co)variance components. Christian (1980) proved that this method is equivalent to SDS. Computer time was less because fewer multiplication operations were needed. The number of addition operations required for this method was not different from SDS. In addition, Christian (1980) suggested that SDS weighted by the inverse of the error variance-covariance matrix among SDS (WSDS) would correct for the inadmissibility (inefficiency) of SDS. However, to complete the analysis by this method as Christian described, it would require

computational steps proportional to n raised to a power of four, where n is the number of observations.

COMPUTING A

The numerator relationship matrix (**A**) is needed for SDS, WSDS, REML, MIVQUE and diagonal MIVQUE under the additive and nonadditive genetic animal model. The computation and storage of this matrix can be costly. Hudson et al. (1982) described a computer algorithm that can compute and use **A** by storing only the diagonal elements and the nonzero off diagonal elements of **A**. This algorithm requires storage for three vectors of order n and two vectors of order equal to the number of nonzero elements of **A**. They found that only 6.6 to 22.6% of the $n(n+1)/2$ elements of the upper triangle of **A** were nonzero for samples from five populations of sires.

UNWEIGHTED MIVQUE

In addition to computational feasibility, it would be convenient if methods of estimating (co)variance components did not depend on the assignment of prior values. Methods such as REML and ML do not depend on the assignment of prior values. Such methods are iterative and can require large amounts of computer time when more than 500 to 1,000 parents are included in a data set especially when the animal model is applied. MIVQUE is not computationally feasible under the animal model with large data sets, and it depends on prior values for its optimal or near-optimal properties.

Rao (1971) suggested that MIVQUE could be applied with all prior (co)variances assigned a value of one including the residual variance so that the experimenter would not have to assign prior values. This

method will be abbreviated MIVQUE(1) in the remainder of this paper. However, this method would not be computationally feasible for the animal model with large data sets.

Brocklebank and Giesbrecht (1984) compared MIVQUE(1) to ANOVA for 4,225 different parameter combinations involving 15 different 2 stage nested designs. For all but one of the 15 designs, MIVQUE(1) resulted in lower standard errors than did ANOVA for more than one-half of the parameter combinations.

CONCLUSIONS

REML or MIVQUE with reasonable priors yield efficient estimates of (co)variance components. However, when the animal model is appropriate, estimates by REML and MIVQUE require too much computer time for large data sets with greater than 500 to 1,000 parents. For additive genetic models, Quaas and Pollack (1980) described a reduced animal model equivalent to the animal model that has MME only for parents of progeny with records. This reduces the size of the MME needed for obtaining BLUP estimates of genic values and for obtaining genic (co)-variance components (Henderson, 1985a, b, c). However, with today's computers it appears not to be feasible to obtain REML or MIVQUE under even the reduced animal model as evidenced by the choices made in the studies of Hudson and Kennedy (1985) and Kennedy et al. (1985). Therefore, the breeder is forced to choose an approximate model and use an efficient method, such as REML as it appears that Kennedy et al. (1985) did, or choose the animal model or RAM and a less efficient, more computationally feasible method for estimating variance components. Hopefully, in the future with improving computer technology and innovative computing shortcuts, this choice will not have to be made.

There is a need to find a computationally feasible algorithm for computing WSDS, and to compare the efficiency of WSDS with other computationally feasible methods such as MIVQUE(0), SDS, and diagonal MIVQUE under the animal model.

THEORY

THE EQUIVALENCE OF MIVQUE AND WEIGHTED SYMMETRIC DIFFERENCES SQUARED

It is shown in this section that Symmetric Differences Squared (SDS) (Grimes and Harvey, 1980) weighted by the inverse of the variance-covariance matrix among squared differences (Y) is MIVQUE (Rao, 1971) when the true parameters are used to construct the Var(Y). The idea of weighting SDS to obtain more efficient estimates of variance components was suggested by other workers (Forthofer and Koch, 1974; Christian, 1980).

Forthofer and Koch (1974) suggested that Symmetric Sums of Products (SSP) (Koch, 1967) might be weighted in some way to obtain more efficient estimates of variance components. Grimes and Harvey (1980) showed that SDS estimates are equivalent to SSP estimates (Koch, 1967) for the one-way classification random model. Christian (1980) suggested that SDS could be corrected for inadmissibility (inefficiency) by weighting by the inverse of the error variance-covariance matrix of Y. While MIVQUE is appropriate for both mixed and random models, SDS was defined only for the random model (Grimes and Harvey, 1980). Therefore, only a random model need be considered when showing the equivalence of MIVQUE and weighted SDS.

The linear model for the phenotypes or observations to be assumed is

$$y = 1_n \mu + \sum_{i=1}^c u_i + e \quad [1]$$

where:

μ is a fixed constant,

n is the total number of observations,

y is an $n \times 1$ vector of observations,

1_n is an $n \times 1$ vector of 1's,

c is the number of random sources of variation not including e ,

and

u_i and e are $n \times 1$ normal random vectors.

The first and second moments of the random effects are:

$$E(e) = E(u_i) = 0,$$

$$\text{Var}(u_i) = V_i \sigma_i^2,$$

$$\text{Var}(e) = I_n \sigma_e^2,$$

$$\text{Cov}(u_i, e') = 0,$$

$$\text{Cov}(u_i, u_j') = 0, \text{ if } i \neq j, \text{ and}$$

$$\text{Var}(y) = \sum_{i=1}^c V_i \sigma_i^2 + I_n \sigma_e^2, \quad [2]$$

where V_i and I_n are known matrices. For example, V_1 might be Wright's numerator relationship matrix and V_2 might be the dominance relationship matrix. σ_i^2 and σ_e^2 represent unknown variance and covariance components. It should be noted that elements within a set of random effects can be correlated in many different ways. However, correlations among random sets of effects are assumed to be zero.

First, the equivalence of MIVQUE and weighted SDS will be shown for a case where the observations are uncorrelated. When all variances and covariances except the residual error variance are assumed to be zero, the observations are uncorrelated. In the second part of the

proof, it is shown that weighted SDS and MIVQUE are equivalent for cases in which correlations exist among observations in y . The vector of observations y is transformed to a random vector y^* whose elements are uncorrelated. It is shown that weighted SDS on y^* results in the same estimates of variance components as weighted SDS on y . Then, applying the first part of the proof for uncorrelated observations in y , weighted SDS on y^* is equivalent to MIVQUE on y^* which is equivalent to MIVQUE on y .

The proof of the equivalence of weighted SDS and MIVQUE can be divided into the following steps.

1. The vector of symmetric differences squared Y is defined using slightly different notation than that of Grimes and Harvey (1980). Y is defined as a vector of squares (HY_1) minus two times a vector of crossproducts (Y_2) .
2. The expectation of Y is given. These expectations are needed to set up the SDS and weighted SDS equations.
3. The equations to solve to obtain estimates of variance components by SDS (unweighted) are given.
4. The variance-covariance matrix for Y is given. The inverse of this matrix is needed to obtain estimates by weighted SDS.
5. The inverse of the error variance-covariance matrix among differences squared in Y is given. Note that this is proportional to the inverse of the variance-covariance matrix of Y if there are no correlations among observations in y .
6. The equations to solve to obtain estimates of variance components by weighted SDS are given.

7. It will be shown that SDS weighted by the inverse of the error variance-covariance matrix of Y (WSDS) is equivalent to MIVQUE(0).
8. Using the results from step 7, it will be shown that SDS weighted by the inverse of the total variance-covariance matrix is equivalent to MIVQUE.

1. Definition of Symmetric Differences Squared

The $q = n(n-1)/2 \times 1$ vector of symmetric differences squared is formed by taking all possible unique differences among observations. These difference are then squared. Define these differences squared as $Y = [(y_1 - y_2)^2 (y_1 - y_3)^2 \dots (y_1 - y_n)^2 (y_2 - y_3)^2 \dots (y_2 - y_n)^2 \dots (y_{n-1} - y_n)^2]'$, which may be written as:

$$Y = [(y_k - y_1)^2] \quad [3]$$

for $k = 1, 2, \dots, n-1; 1 = k + 1, k + 2, \dots, n$.

Expand the squares in [3] and express Y as a vector of squares (HY_1) minus two times a vector of crossproducts Y_2 in [4].

$$\begin{aligned} Y &= [y_k^2 - 2y_k y_1 + y_1^2] \\ &= [y_k^2 + y_1^2] - 2[y_k y_1] \\ &= HY_1 - 2Y_2 \end{aligned} \quad [4]$$

where:

$$Y_1 = [y_1^2 \ y_2^2 \ \dots \ y_n^2]', \text{ and} \quad [5]$$

$$Y_2 = [y_1 y_2 \ y_1 y_3 \ \dots \ y_1 y_n \ y_2 y_3 \ \dots \ y_{n-1} y_n]' \quad [6]$$

H is a $q \times n$ matrix containing zeros and ones, which specifies the elements of Y_1 to be incorporated into Y . It is defined as

$$H = \begin{bmatrix} 1 & 1 & 0 & 0 & . & . & . & 0 & 0 \\ 1 & 0 & 1 & 0 & . & . & . & 0 & 0 \\ . & . & . & . & & & & . & . \\ . & . & . & . & & & & . & . \\ . & . & . & . & & & & . & . \\ 1 & 0 & 0 & 0 & . & . & . & 0 & 1 \\ 0 & 1 & 1 & 0 & . & . & . & 0 & 0 \\ . & . & . & . & & & & . & . \\ . & . & . & . & & & & . & . \\ . & . & . & . & & & & . & . \\ 0 & 0 & 0 & 0 & . & . & . & 1 & 1 \end{bmatrix} . \quad [7]$$

There are three useful matrix identities involving H that will be needed in the proof that follows. These are

$$H1_n = 21_q, \quad [8]$$

$$H'1_q = (n-1)1_n, \text{ and} \quad [9]$$

$$H'H = (n-2)I_n + 1_n1_n'. \quad [10]$$

Identity [8] can be explained by noting that every row of H has two ones and $n-2$ zeros. Likewise, identity [9] can be explained by noting that every column of H has $n-1$ ones and $(n-1)(n-2)/2$ zeros. The diagonals of [10] are all $n-1$ because each column of H has $n-1$ ones and $(n-1)(n-2)/2$ zeros. Each of the off-diagonal elements of [10] is one because each pair of columns of H has a one in the same row only one time.

2. Expectation of Symmetric Differences Squared

The expected value of Y ($E(Y)$) is needed to set up the SDS and weighted SDS equations. $E(Y)$ is written as a function of unknown variance components and the elements of V_i as follows:

$$E(Y) = E(HY_1 - 2Y_2) = HE(Y_1) - 2E(Y_2). \quad [11]$$

The expected value of Y_1 is

$$E(Y_1) = 1_n\mu^2 + X_1\sigma^2 \quad [12]$$

where:

$$\sigma^2 = [\sigma_1^2 \sigma_2^2 \dots \sigma_c^2 \sigma_e^2]', \quad [13]$$

$$X_1 = \begin{bmatrix} (v_{11})_1 & (v_{11})_2 & \dots & (v_{11})_c & 1 \\ (v_{22})_1 & (v_{22})_2 & \dots & (v_{22})_c & 1 \\ \vdots & \vdots & & \vdots & \vdots \\ \vdots & \vdots & & \vdots & \vdots \\ (v_{nn})_1 & (v_{nn})_2 & \dots & (v_{nn})_c & 1 \end{bmatrix}, \text{ and} \quad [14]$$

$(v_{kk})_i$ is the k^{th} diagonal element of V_i .

The expected value of Y_2 is

$$E(Y_2) = 1_q \mu^2 + X_2 \sigma^2, \quad [15]$$

where

$$X_2 = \begin{bmatrix} (v_{12})_1 & (v_{12})_2 & \dots & (v_{12})_c & 0 \\ (v_{13})_1 & (v_{13})_2 & \dots & (v_{13})_c & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ \vdots & \vdots & & \vdots & \vdots \\ (v_{1n})_1 & (v_{1n})_2 & \dots & (v_{1n})_c & 0 \\ (v_{23})_1 & (v_{23})_2 & \dots & (v_{2n})_c & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ \vdots & \vdots & & \vdots & \vdots \\ (v_{2n})_1 & (v_{2n})_2 & \dots & (v_{2n})_c & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ \vdots & \vdots & & \vdots & \vdots \\ (v_{n-1,n})_1 & (v_{n-1,n})_2 & \dots & (v_{n-1,n})_c & 0 \end{bmatrix}, \text{ and} \quad [16]$$

$(v_{kl})_i$ is the element in the k^{th} row and l^{th} column of V_i .

It should be noted that when there is no inbreeding, X_1 is

$$X_1 = 1_n 1'_{c+1}. \quad [17]$$

Substitute [12] and [15] into [11] and the $E(Y)$ can be written as:

$$E(Y) = H 1_n \mu^2 + H X_1 \sigma^2 - 2 1_q \mu^2 - 2 X_2 \sigma^2. \quad [18]$$

Substitute [8] into [18] and $E(Y)$ can be written as:

$$E(Y) = 2 1_q \mu^2 + H X_1 \sigma^2 - 2 1_q \mu^2 - 2 X_2 \sigma^2, \text{ which, after}$$

combining terms and rearrangement is

$$\begin{aligned} E(Y) &= (HX_1 - 2X_2)\sigma^2, \text{ or} \\ &= X\sigma^2, \end{aligned}$$

where

$$X = HX_1 - 2X_2. \quad [19]$$

3. Symmetric Differences Squared Equations

Estimates of variance and covariance components can be obtained by solving

$$X'X\sigma^2 = X'Y. \quad [20]$$

It should be emphasized that [20] are the same equations as used by Grimes and Harvey (1980) to obtain estimates of variance components.

4. The Variance - Covariance Matrix Among Symmetric Differences Squared

The inverse of the variance-covariance matrix of Y is needed to obtain estimates of variance components by weighted SDS. Define $\text{Var}(Y)$ as

$$\begin{aligned} \text{Var}(Y) &= \text{Cov}(Y, Y'), \\ &= [\text{Cov}\{(y_k - y_1)^2, (y_m - y_0)^2\}], \text{ or} \\ &= 2[(v_{km} - v_{lm} - v_{ko} + v_{lo})^2], \quad [21] \end{aligned}$$

for $k = 1, 2, \dots, n-1; l = k+1, k+2, \dots, n,$

and

$m = 1, 2, \dots, n-1; o = m+1, m+2, \dots, n,$

where v_{km} is the element in the k^{th} row and the m^{th} column of $\text{Var}(y) = V$.

The inverse of [21] is difficult to represent algebraically because V can be any positive definite nonsingular matrix. Fortunately, this inverse is not needed to accomplish the objectives of this paper.

First, the inverse of [21] will be obtained for the special case when V is proportional to I_n , which can be written as:

$$V \propto I_n.$$

It will then be shown that even when $\text{Var}(\mathbf{y})$ is complicated, \mathbf{y} can be transformed to a \mathbf{y}^* with a variance proportional to I_n , and that estimates of variance and covariance components by MIVQUE and weighted SDS are identical whether the analyses are completed on \mathbf{y} or \mathbf{y}^* .

The variance of \mathbf{Y} can be rewritten as

$$\begin{aligned} \text{Var}(\mathbf{Y}) &= \text{Var}(\mathbf{H}\mathbf{Y}_1 - 2\mathbf{Y}_2) \\ &= \text{Cov}(\mathbf{H}\mathbf{Y}_1 - 2\mathbf{Y}_2, \mathbf{Y}_1'\mathbf{H}' - 2\mathbf{Y}_2') \\ &= \text{Cov}(\mathbf{H}\mathbf{Y}_1, \mathbf{Y}_1'\mathbf{H}') - 2\text{Cov}(\mathbf{H}\mathbf{Y}_1, \mathbf{Y}_2') - 2\text{Cov}(\mathbf{Y}_2, \mathbf{Y}_1'\mathbf{H}') + 4\text{Cov}(\mathbf{Y}_2, \mathbf{Y}_2'), \text{ or} \\ &= \mathbf{H} \text{Var}(\mathbf{Y}_1)\mathbf{H}' - 2 \mathbf{H} \text{Cov}(\mathbf{Y}_1, \mathbf{Y}_2') - 2\text{Cov}(\mathbf{Y}_2, \mathbf{Y}_1')\mathbf{H}' + 4\text{Var}(\mathbf{Y}_2). \quad [22] \end{aligned}$$

When all variance and covariance components except σ_e^2 are assumed to be zero, the second moments involving \mathbf{Y}_1 and \mathbf{Y}_2 are

$$\text{Var}(\mathbf{Y}_1) = 2 \sigma_e^4 \mathbf{I}_n, \quad [23]$$

$$\text{Var}(\mathbf{Y}_2) = \sigma_e^4 \mathbf{I}_q, \quad [24]$$

$$\text{Cov}(\mathbf{Y}_1, \mathbf{Y}_2') = \mathbf{0}_{nq}, \text{ and} \quad [25]$$

$$\text{Cov}(\mathbf{Y}_2, \mathbf{Y}_1') = \mathbf{0}_{qn}. \quad [26]$$

Substitute [23], [24], [25], and [26] into [22] and the $\text{Var}(\mathbf{Y})$ is

$$\begin{aligned} \text{Var}(\mathbf{Y}) &= 2 \sigma_e^4 \mathbf{H}\mathbf{H}' + 4 \sigma_e^4 \mathbf{I}_q, \\ &= 2 \sigma_e^4 (\mathbf{H}\mathbf{H}' + 2\mathbf{I}_q), \text{ or} \\ &= 2 \sigma_e^4 \mathbf{W}, \end{aligned}$$

when σ_e^2 is the only nonzero prior value, where

$$\mathbf{W} = (\mathbf{H}\mathbf{H}' + 2\mathbf{I}_q). \quad [27]$$

It should be noted that SDS weighted by the inverse of \mathbf{W} is equivalent to SDS weighted by the inverse of $\text{Var}(\mathbf{Y})$ if

$$W \propto \text{Var}(\mathbf{Y}).$$

It should be emphasized that

$$\text{Var}(\mathbf{Y}) \propto W$$

whenever

$$\text{Var}(\mathbf{y}) \propto \mathbf{I}_n.$$

This is true if all variance components except σ_e^2 are assumed to be zero, or if \mathbf{y} is a random vector with variance proportional to \mathbf{I}_n .

5. The Inverse of the Error Variance - Covariance Matrix of \mathbf{Y}

The inverse of W can be written as:

$$W^{-1} = (\mathbf{H}\mathbf{H}' + 2\mathbf{I}_q)^{-1}. \quad [28]$$

Now, let us apply equation [17] of Henderson and Searle (1981) to find the inverse of the sum of 2 matrices. Their equation [17] is

$$(\mathbf{A} + \mathbf{U}\mathbf{B}\mathbf{U}')^{-1} = \mathbf{A}^{-1} - \mathbf{A}^{-1}\mathbf{U}(\mathbf{B}^{-1} + \mathbf{U}'\mathbf{A}^{-1}\mathbf{U})^{-1}\mathbf{U}'\mathbf{A}^{-1} \quad [29]$$

If we let $\mathbf{A} = 2\mathbf{I}_q$

$\mathbf{U} = \mathbf{H}$, and

$\mathbf{B} = \mathbf{I}_n$, and substitute into [29],

W^{-1} can be written as

$$W^{-1} = \left[\frac{1}{2}\mathbf{I}_q - \frac{1}{2}\mathbf{H}(\mathbf{I}_n + \frac{1}{2}\mathbf{H}'\mathbf{H})^{-1}\mathbf{H}' \frac{1}{2} \right]. \quad [30]$$

After rearrangement, [30] is

$$W^{-1} = \frac{1}{2} [\mathbf{I}_q - \mathbf{H}(2\mathbf{I}_n + \mathbf{H}'\mathbf{H})^{-1}\mathbf{H}']. \quad [31]$$

Substitute [10] into [31], and observe that

$$\begin{aligned} (2\mathbf{I}_n + \mathbf{H}'\mathbf{H})^{-1} &= (2\mathbf{I}_n + (n-2)\mathbf{I}_n + \mathbf{1}_n\mathbf{1}_n')^{-1}, \text{ or after combining terms,} \\ &= (n\mathbf{I}_n + \mathbf{1}_n\mathbf{1}_n')^{-1}. \end{aligned} \quad [32]$$

Now we can apply equation [3] of Henderson and Searle (1981) to

evaluate [32]. Their equation [3] is

$$(A + buv')^{-1} = A^{-1} - \frac{b}{1 + bv'A^{-1}u} A^{-1}uv'A^{-1}. \quad [33]$$

We let

$$A = nI_n,$$

$$u = 1_n,$$

$$v' = 1_n',$$

$$b = 1,$$

and substitute into [33] to obtain

$$(nI_n + 1_n 1_n')^{-1} = \frac{1}{n} I_n - \frac{1}{(1 + \frac{1}{n} 1_n' 1_n)} (\frac{1}{n}) 1_n 1_n' \frac{1}{n},$$

which after simplification is

$$= \frac{1}{n} (I_n - \frac{1}{2n} 1_n 1_n'). \quad [34]$$

Substitute [34] into [31] to obtain

$$W^{-1} = \frac{1}{2} [I_q - \frac{1}{n} H(I_n - \frac{1}{2n} 1_n 1_n')H'], \text{ which}$$

simplifies after rearrangement to

$$W^{-1} = \frac{1}{2} [I_q - \frac{1}{n} HH' + \frac{2}{n^2} 1_q 1_q']. \quad [35]$$

6. Weighted Symmetric Differences Squared Equations

Estimates of variance components by weighted SDS can be obtained by solving

$$X'W^{-1}X\sigma^2 = X'W^{-1}Y. \quad [36]$$

The solution to [36] yields the same estimates that Christian (1980)

suggested after correcting SDS for inquadmissibility.

7. The Equivalence of SDS Weighted by the Inverse of the Error Variance-Covariance Matrix and MIVQUE(0)

It will now be shown that the solution to [36] is equivalent to MIVQUE if all variances and covariances except σ_e^2 are zero, or if $\text{Var}(\mathbf{y}) \propto \mathbf{I}_n$. It will first be shown that

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{X} = [\text{tr}(\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{V}_j)], \quad [37]$$

for

$$(i, j = 1, 2, \dots, c, c+1),$$

where

$$\begin{aligned} \mathbf{V}_{c+1} &= \mathbf{I}_n, \\ \mathbf{M} &= \mathbf{I}_n - \frac{1}{n} \mathbf{1}_n \mathbf{1}_n', \end{aligned} \quad [38]$$

and

$$[\text{tr}(\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{V}_j)]$$

is a $(c + 1) \times (c + 1)$ matrix that contains the left hand side of equations used by Rao (1971) to obtain MIVQUE(0) estimates of variance and covariance components. It will then be shown that

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y} = [\mathbf{y}'\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{y}], \quad [39]$$

for

$$(i = 1, 2, \dots, c, c + 1),$$

where $[\mathbf{y}'\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{y}]$ is a $(c + 1) \times 1$ vector that is the right hand side of the equations used by Rao (1971) to obtain MIVQUE(0) estimates of variance components. Let estimates of variance components by MIVQUE(0) and SDS weighted by \mathbf{W}^{-1} be denoted by $\hat{\sigma}^2$ and $\hat{\sigma}^2$, respectively, where

$$\hat{\sigma}^2 = (\mathbf{X}'\mathbf{W}^{-1}\mathbf{X})^{-1}\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y}, \quad [40]$$

and

$$\hat{\sigma}^2 = [\text{tr}(\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{V}_j)]^{-1}[\mathbf{Y}'\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{Y}]. \quad [41]$$

Therefore, if equalities [37] and [39] are true then [37] and [39] can be substituted into [40] to obtain

$$\hat{\sigma}^2 = [\text{tr}(\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{V}_j)]^{-1}[\mathbf{Y}'\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{Y}],$$

which after applying [41] is

$$\hat{\sigma}^2 = \hat{\sigma}^2.$$

Therefore, if equalities [37] and [39] are true and if $\text{Var}(\mathbf{y}) \propto \mathbf{I}_n$, estimates of variance components by MIVQUE and SDS weighted by \mathbf{W}^{-1} are equivalent.

If [35] is substituted into [36], the left hand sides of [36] are

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{X} = \frac{1}{2} (\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2') [\mathbf{I}_q - \frac{1}{n} \mathbf{H}\mathbf{H}' + \frac{2}{n^2} \mathbf{1}_q\mathbf{1}_q'] (\mathbf{H}\mathbf{X}_1 - 2\mathbf{X}_2),$$

which after expanding through the center parentheses can be written as:

$$\begin{aligned} &= \frac{1}{2} [(\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2')(\mathbf{H}\mathbf{X}_1 - 2\mathbf{X}_2) \\ &\quad - \frac{1}{n} (\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2')\mathbf{H}\mathbf{H}'(\mathbf{H}\mathbf{X}_1 - 2\mathbf{X}_2) \\ &\quad + \frac{2}{n^2} (\mathbf{X}_1' - 2\mathbf{X}_2')\mathbf{1}_q\mathbf{1}_q'(\mathbf{H}\mathbf{X}_1 - 2\mathbf{X}_2)]. \end{aligned} \quad [42]$$

The first term within the brackets of [42] is

$$(\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2')(\mathbf{H}\mathbf{X}_1 - 2\mathbf{X}_2) = \mathbf{X}_1'\mathbf{H}'\mathbf{H}\mathbf{X}_1 - 2\mathbf{X}_2'\mathbf{H}\mathbf{X}_1 - 2\mathbf{X}_1'\mathbf{H}'\mathbf{X}_2 + 4\mathbf{X}_2'\mathbf{X}_2,$$

which after substituting [10] for $\mathbf{H}'\mathbf{H}$ simplifies to

$$(n-2)\mathbf{X}_1'\mathbf{X}_1 + \mathbf{X}_1'\mathbf{1}_n\mathbf{1}_n'\mathbf{X}_1 - 2\mathbf{X}_2'\mathbf{H}\mathbf{X}_1 - 2\mathbf{X}_1'\mathbf{H}'\mathbf{X}_2 + 4\mathbf{X}_2'\mathbf{X}_2. \quad [43]$$

It should be noted that [43] is the same as the left hand side of the SDS equations used by Grimes and Harvey (1980) to obtain estimates of variance and covariance components.

The second term within the brackets of [42] is $1/n$ multiplied by

$$(X_1'H' - 2X_2')HH'(HX_1 - 2X_2) = X_1'H'HH'HX_1 - 2X_1'H'HH'X_2 \\ - 2X_2'HH'HX_1 + 4X_2'HH'X_2,$$

which after substituting [10] for $H'H$ simplifies to

$$(n-2)^2X_1'X_1 + (3n-4)X_1'l_n l_n'X_1 - 2(n-2)X_1'H'X_2 \\ - 4X_1'l_n l_q'X_2 - 2(n-2)X_2'HX_1 - 4X_2'l_q l_n'X_1 + 4X_2'HH'X_2. \quad [44]$$

The third term within the brackets of [42] is $2/n^2$ multiplied by

$$(X_1'H' - 2X_2')l_q l_q'(HX_1 - 2X_2) = X_1'H'l_q l_q'HX_1 - 2X_1'H'l_q l_q'X_2 - 2X_2'l_q l_q'HX_1 \\ + 4X_2'l_q l_q'X_2,$$

which after substituting [9] for $H'l_q$ simplifies to

$$(X_1'H' - 2X_2')l_q l_q'(HX_1 - 2X_2) = (n-1)^2X_1'l_n l_n'X_1 - 2(n-1)X_1'l_n l_q'X_2 \\ - 2(n-1)X_2'l_q l_n'X_1 + 4X_2'l_q l_q'X_2. \quad [45]$$

We can substitute [43], [44], and [45] into [42] to obtain

$$X'W^{-1}X = \frac{1}{2} \{ (n-2)X_1'X_1 + X_1'l_n l_n'X_1 - 2X_2'HX_1 - 2X_1'H'X_2 + 4X_2'X_2 \\ - \frac{1}{n} [(n-2)^2X_1'X_1 + (3n-4)X_1'l_n l_n'X_1 - 2(n-2)X_1'H'X_2 \\ - 4X_1'l_n l_q'X_2 - 2(n-2)X_2'HX_1 - 4X_2'l_q l_n'X_1 + 4X_2'HH'X_2] \\ + \frac{2}{n^2} [(n-1)^2 X_1'l_n l_n'X_1 - 2(n-1)X_1'l_n l_q'X_2 \\ - 2(n-1) X_2'l_q l_n'X_1 + 4X_2'l_q l_q'X_2] \}, \quad [46]$$

or

$$\begin{aligned}
\mathbf{X}'\mathbf{W}^{-1}\mathbf{X} = & \frac{(n-2)}{n} \mathbf{X}_1'\mathbf{X}_1 + \frac{1}{n^2} \mathbf{X}_1'\mathbf{1}_n\mathbf{1}_n'\mathbf{X}_1 - \frac{2}{n} \mathbf{X}_2'\mathbf{H}\mathbf{X}_1 - \frac{2}{n} \mathbf{X}_1'\mathbf{H}'\mathbf{X}_2 + 2\mathbf{X}_2'\mathbf{X}_2 \\
& + \frac{2}{n^2} \mathbf{X}_1'\mathbf{1}_n\mathbf{1}_q'\mathbf{X}_2 + \frac{2}{n^2} \mathbf{X}_2'\mathbf{1}_q\mathbf{1}_n'\mathbf{X}_1 - \frac{2}{n} \mathbf{X}_2'\mathbf{H}\mathbf{H}'\mathbf{X}_2 + \frac{4}{n^2} \mathbf{X}_2'\mathbf{1}_q\mathbf{1}_q'\mathbf{X}_2, \quad [47]
\end{aligned}$$

which after further rearrangement is

$$\begin{aligned}
\mathbf{X}'\mathbf{W}^{-1}\mathbf{X} = & (\mathbf{X}_1'\mathbf{X}_1 + 2\mathbf{X}_2'\mathbf{X}_2) \\
& - \frac{2}{n} (\mathbf{X}_2'\mathbf{H} + \mathbf{X}_1')(\mathbf{H}'\mathbf{X}_2 + \mathbf{X}_1) \\
& + \frac{1}{n^2} (\mathbf{X}_1'\mathbf{1}_n + 2\mathbf{X}_2'\mathbf{1}_q)(\mathbf{1}_n'\mathbf{X}_1 + 2\mathbf{1}_q'\mathbf{X}_2). \quad [48]
\end{aligned}$$

The following matrix equalities are useful:

$$[\text{tr}(\mathbf{V}_i\mathbf{V}_j)] = \mathbf{X}_i'\mathbf{X}_j + 2\mathbf{X}_i'\mathbf{X}_j, \quad [49]$$

for $i, j = 1, 2, \dots, c+1$,

$$[\mathbf{1}_n'\mathbf{V}_j\mathbf{1}_n] = \mathbf{1}_n'\mathbf{X}_j + 2\mathbf{1}_q'\mathbf{X}_j, \quad [50]$$

and

$$[\mathbf{1}_n'\mathbf{V}_j\mathbf{1}_n] = \mathbf{1}_n'\mathbf{X}_j + 2\mathbf{1}_q'\mathbf{X}_j. \quad [51]$$

Equalities [49] through [51] are proven in Appendix A. Substitute [49] through [51] into [48] to obtain

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{X} = [\text{tr}(\mathbf{V}_i\mathbf{V}_j)] - \frac{2}{n} [\text{tr}(\mathbf{1}_n'\mathbf{V}_i\mathbf{V}_j\mathbf{1}_n)] + \frac{1}{n^2} [\text{tr}(\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n\mathbf{1}_n'\mathbf{V}_j\mathbf{1}_n)], \text{ which}$$

after rotating traces is

$$\begin{aligned}
= & [\text{tr}(\mathbf{V}_i\mathbf{V}_j)] - \frac{1}{n} [\text{tr}(\mathbf{V}_i\mathbf{1}_n\mathbf{1}_n'\mathbf{V}_j)] - \frac{1}{n} [\text{tr}(\mathbf{1}_n\mathbf{1}_n'\mathbf{V}_i\mathbf{V}_j)] \\
& + \frac{1}{n^2} [\text{tr}(\mathbf{1}_n\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n\mathbf{1}_n'\mathbf{V}_j)], \text{ or}
\end{aligned}$$

$$\begin{aligned}
\mathbf{X}'\mathbf{W}^{-1}\mathbf{X} &= \{\text{tr}[\mathbf{V}_i\mathbf{V}_j - \frac{1}{n} \mathbf{V}_i\mathbf{1}_n\mathbf{1}_n'\mathbf{V}_j - \frac{1}{n} \mathbf{1}_n\mathbf{1}_n'\mathbf{V}_i\mathbf{V}_j + \frac{1}{n^2} \mathbf{1}_n\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n\mathbf{1}_n'\mathbf{V}_j]\}, \\
&= \{\text{tr}[\mathbf{V}_i(\mathbf{V}_j - \frac{1}{n} \mathbf{1}_n\mathbf{1}_n'\mathbf{V}_j) - \frac{1}{n} \mathbf{1}_n\mathbf{1}_n'\mathbf{V}_i(\mathbf{V}_j - \frac{1}{n} \mathbf{1}_n\mathbf{1}_n'\mathbf{V}_j)]\}, \\
&= \{\text{tr}[(\mathbf{V}_i - \frac{1}{n} \mathbf{1}_n\mathbf{1}_n'\mathbf{V}_i)(\mathbf{V}_j - \frac{1}{n} \mathbf{1}_n\mathbf{1}_n'\mathbf{V}_j)]\}, \\
&= \{\text{tr}[(\mathbf{I}_n - \frac{1}{n} \mathbf{1}_n\mathbf{1}_n')\mathbf{V}_i(\mathbf{I}_n - \frac{1}{n} \mathbf{1}_n\mathbf{1}_n')\mathbf{V}_j]\}. \tag{52}
\end{aligned}$$

Finally, substitute [38] into [52] to obtain

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{X} = \text{tr}(\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{V}_j), \text{ which proves [37].}$$

Substitute [35] into the right hand sides of [36] to obtain

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y} = \frac{1}{2} (\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2')[\mathbf{I}_q - \frac{1}{n} \mathbf{H}\mathbf{H}' + \frac{2}{n^2} \mathbf{1}_q\mathbf{1}_q'](\mathbf{H}\mathbf{Y}_1 - 2\mathbf{Y}_2),$$

which after expanding through the center parentheses becomes

$$\begin{aligned}
\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y} &= \frac{1}{2} [(\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2')(\mathbf{H}\mathbf{Y}_1 - 2\mathbf{Y}_2) \\
&\quad - \frac{1}{n} (\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2')\mathbf{H}\mathbf{H}'(\mathbf{H}\mathbf{Y}_1 - 2\mathbf{Y}_2) \\
&\quad + \frac{2}{n^2} (\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2')\mathbf{1}_q\mathbf{1}_q'(\mathbf{H}\mathbf{Y}_1 - 2\mathbf{Y}_2)]. \tag{53}
\end{aligned}$$

The first term within the brackets of [53] is

$$(\mathbf{X}_1'\mathbf{H}' - 2\mathbf{X}_2')(\mathbf{H}\mathbf{Y}_1 - 2\mathbf{Y}_2) = \mathbf{X}_1'\mathbf{H}'\mathbf{H}\mathbf{Y}_1 - 2\mathbf{X}_2'\mathbf{H}\mathbf{Y}_1 - 2\mathbf{X}_1'\mathbf{H}'\mathbf{Y}_2 + 4\mathbf{X}_2'\mathbf{Y}_2,$$

which after substituting [10] for $\mathbf{H}'\mathbf{H}$ simplifies to

$$(n-2)\mathbf{X}_1'\mathbf{Y}_1 + \mathbf{X}_1'\mathbf{1}_n\mathbf{1}_n'\mathbf{Y}_1 - 2\mathbf{X}_2'\mathbf{H}\mathbf{Y}_1 - 2\mathbf{X}_1'\mathbf{H}'\mathbf{Y}_2 + 4\mathbf{X}_2'\mathbf{Y}_2. \tag{54}$$

It should be noted that [54] is the same as the right hand side of the SDS equations used by Grimes and Harvey (1980) to obtain estimates of

variance and covariance components.

The second term within the brackets of [53] is $\frac{1}{n}$ multiplied by

$$(X_1'H' - 2X_2')HH'(HY_1 - 2Y_2) = X_1'H'HH'HY_1 - 2X_1'H'HH'Y_2 \\ - 2X_2'HH'HY_1 + 4X_2'HH'Y_2,$$

which after substituting [10] for $H'H$ simplifies to

$$(n-2)^2X_1'Y_1 + (3n-4)X_1'l_n l_n'Y - 2(n-2)X_1'H'Y_2 \\ - 4X_1'l_n l_q'Y_2 - 2(n-2)X_2'HY_1 - 4X_2'l_q l_n'Y_1 + 4X_2'HH'Y_2 \quad [55]$$

The third term within the brackets of [53] is $\frac{2}{n^2}$ multiplied by

$$(X_1'H' - 2X_2')l_q l_q'(HY_1 - 2Y_2) = X_1'H'l_q l_q'HY_1 - 2X_1'H'l_q l_q'Y_2 - 2X_2'l_q l_q'HY_1 \\ + 4X_2'l_q l_q'Y_2,$$

which after substituting [9] for $H'l_q$ simplifies to

$$(n-1)^2X_1'l_n l_n'Y_1 - 2(n-1)X_1'l_n l_q'Y_2 \\ - 2(n-1)X_2'l_q l_n'Y_1 + 4X_2'l_q l_q'Y_2. \quad [56]$$

We can substitute [54] through [56] into [53] to obtain (after simplification)

$$X'W^{-1}Y = \frac{(n-2)}{n} X_1'Y_1 + \frac{1}{n^2} X_1'l_n l_n'Y_1 - \frac{2}{n} X_2'HY_1 - \frac{2}{n} X_1'H'Y_2 + 2X_2'Y_2 \\ + \frac{2}{n^2} X_1'l_n l_q'Y_2 + \frac{2}{n^2} X_2'l_q l_n'Y_1 - \frac{2}{n} X_2'HH'Y_2 + \frac{4}{n^2} X_2'l_q l_q'Y_2, \quad [57]$$

which after further rearrangement is

$$\begin{aligned}
\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y} &= (\mathbf{X}_1'\mathbf{Y}_1 + 2\mathbf{X}_2'\mathbf{Y}_2) \\
&\quad - \frac{2}{n} (\mathbf{X}_2'\mathbf{H} + \mathbf{X}_1')(\mathbf{H}'\mathbf{Y}_2 + \mathbf{Y}_1) \\
&\quad + \frac{1}{n^2} (\mathbf{X}_1'\mathbf{l}_n + 2\mathbf{X}_2'\mathbf{l}_q)(\mathbf{l}_n'\mathbf{Y}_1 + 2\mathbf{l}_q'\mathbf{Y}_2).
\end{aligned} \tag{58}$$

The following matrix equalities are useful:

$$[\mathbf{Y}'\mathbf{V}_i\mathbf{Y}] = \mathbf{X}_1'\mathbf{Y}_1 + 2\mathbf{X}_2'\mathbf{Y}_2, \tag{59}$$

$$\mathbf{Y}\mathbf{Y}'\mathbf{l}_n = \mathbf{H}'\mathbf{Y}_2 + \mathbf{Y}_1, \tag{60}$$

and

$$\mathbf{l}_n'\mathbf{Y}\mathbf{Y}'\mathbf{l}_n = \mathbf{l}_n'\mathbf{Y}_1 + 2\mathbf{l}_q'\mathbf{Y}_2. \tag{61}$$

Proofs of [59] through [61] are in Appendix A.

We can substitute [59] through [61] into [58] to obtain

$$\begin{aligned}
\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y} &= [\mathbf{Y}'\mathbf{V}_i\mathbf{Y} - \frac{2}{n} \mathbf{l}_n'\mathbf{V}_i\mathbf{Y}\mathbf{Y}'\mathbf{l}_n + \mathbf{l}_n'\mathbf{V}_i\mathbf{l}_n\mathbf{l}_n'\mathbf{Y}\mathbf{Y}'\mathbf{l}_n], \\
&= [\mathbf{Y}'\mathbf{V}_i\mathbf{Y} - \frac{1}{n} \mathbf{Y}'\mathbf{V}_i\mathbf{l}_n\mathbf{l}_n'\mathbf{Y} - \frac{1}{n} \mathbf{Y}'\mathbf{l}_n\mathbf{l}_n'\mathbf{V}_i\mathbf{Y} + \frac{1}{n^2} \mathbf{Y}'\mathbf{l}_n\mathbf{l}_n'\mathbf{V}_i\mathbf{l}_n\mathbf{l}_n'\mathbf{Y}], \\
&= [\mathbf{Y}'\mathbf{V}_i(\mathbf{Y} - \frac{1}{n} \mathbf{l}_n\mathbf{l}_n'\mathbf{Y}) - \frac{1}{n} \mathbf{Y}'\mathbf{l}_n\mathbf{l}_n'\mathbf{V}_i(\mathbf{Y} - \frac{1}{n} \mathbf{l}_n\mathbf{l}_n'\mathbf{Y})], \\
&= [(\mathbf{Y}'\mathbf{V}_i - \frac{1}{n} \mathbf{Y}'\mathbf{l}_n\mathbf{l}_n'\mathbf{V}_i)(\mathbf{Y} - \frac{1}{n} \mathbf{l}_n\mathbf{l}_n'\mathbf{Y})], \\
&= [(\mathbf{Y}' - \frac{1}{n} \mathbf{Y}'\mathbf{l}_n\mathbf{l}_n')\mathbf{V}_i(\mathbf{Y} - \frac{1}{n} \mathbf{l}_n\mathbf{l}_n'\mathbf{Y})], \\
&= [\mathbf{Y}'(\mathbf{I}_n - \frac{1}{n} \mathbf{l}_n\mathbf{l}_n')\mathbf{V}_i(\mathbf{I}_n - \frac{1}{n} \mathbf{l}_n\mathbf{l}_n')\mathbf{Y}]
\end{aligned} \tag{62}$$

Finally, substitute [38] into [62] to obtain

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y} = [\mathbf{Y}'\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{Y}],$$

to prove equality [39].

Therefore, it is shown that the equations for computing estimates of variance and covariance components by MIVQUE are equivalent to SDS equations weighted by the inverse of $\text{Var}(\mathbf{y})$ if the $\text{Var}(\mathbf{y}) \propto \mathbf{I}_n$. Since the equations are equivalent then so are the estimates of variance components.

8. The Equivalence of SDS Weighted by the Inverse of the Total Variance-Covariance Matrix and MIVQUE

Now it will be shown that MIVQUE and weighted SDS are equivalent even when $\text{Var}(\mathbf{y})$ is not proportional to \mathbf{I}_n . One strategy is to obtain a transformation of \mathbf{y} , say \mathbf{Ty} such that $\text{Var}(\mathbf{Ty}) = \mathbf{I}_n$, and then show that weighted SDS completed on \mathbf{Ty} is equivalent to MIVQUE. This is the procedure to be followed here. Let $\mathbf{V} = \mathbf{LDL}'$, where $\mathbf{L}'\mathbf{L} = \mathbf{I}_n$ and \mathbf{D} is a diagonal matrix of positive real numbers. Then, the inverse of \mathbf{V} is

$$\mathbf{V}^{-1} = \mathbf{LD}^{-1}\mathbf{L}'. \quad [63]$$

If we obtain the transformation of $\mathbf{y} \rightarrow \mathbf{Ty}$, and let

$$\mathbf{T} = \mathbf{D}^{-1/2}\mathbf{L}', \quad [64]$$

\mathbf{V}^{-1} can be written as a function of \mathbf{T} as follows:

$$\mathbf{V}^{-1} = \mathbf{LD}^{-1/2}\mathbf{D}^{-1/2}\mathbf{L}' = \mathbf{T}'\mathbf{T}. \quad [65]$$

The variance of \mathbf{Ty} is

$$\begin{aligned} \text{Var}(\mathbf{Ty}) &= \mathbf{TVT}', \\ &= \mathbf{D}^{-1/2}\mathbf{L}'\mathbf{LDL}'\mathbf{D}^{-1/2} = \mathbf{I}_n, \text{ or} \\ &= \sum_i \sigma_i^2 \mathbf{T}\mathbf{V}_i\mathbf{T}' + \sigma_e^2 \mathbf{D}^{-1}. \end{aligned} \quad [66]$$

There are two important points to be made here. First, $\text{Var}(\mathbf{Ty}) \propto \mathbf{I}_n$ so that the results given previously on the equivalence of weighted SDS and MIVQUE are valid when the analysis is on \mathbf{Ty} . Second, the $\text{Var}(\mathbf{Ty})$

[66] is written in terms of the same unknown parameters as the $\text{Var}(\mathbf{y})$ [2].

Let us denote the vector of transformed observations as

$$\mathbf{y}^* = \mathbf{T}\mathbf{y} = [y_1^* \ y_2^* \ \dots \ y_n^*]', \text{ and} \quad [67]$$

the vector of symmetric differences squared as

$$\mathbf{Y}^* = [(y_k^* - y_l^*)^2], \text{ for} \quad [68]$$

$$(k = 1, 2, \dots, n-1; \ l = k+1, k+2, \dots, n).$$

The columns of \mathbf{X}_1^* are now the diagonals of $\mathbf{T}\mathbf{V}_1\mathbf{T}'$ and \mathbf{D}^{-1} instead of the diagonals of \mathbf{V}_1 and \mathbf{I}_n . Also, the columns of \mathbf{X}_2^* are the q off diagonal elements of $\mathbf{T}\mathbf{V}_1\mathbf{T}'$ and \mathbf{D}^{-1} instead of the off diagonal elements of \mathbf{V}_1 and \mathbf{I}_n . Hence,

$$\text{Var}(\mathbf{Y}^*) = 2\mathbf{W}^* = (\mathbf{H}\mathbf{H}' + 2\mathbf{I}_q), \text{ and} \quad [69]$$

$$\mathbf{W}^{*-1} = \frac{1}{2} \left[\mathbf{I}_q - \frac{1}{n} \mathbf{H}\mathbf{H}' + \frac{2}{n^2} \mathbf{1}_q \mathbf{1}_q' \right]. \quad [70]$$

\mathbf{W}^{*-1} [70] is identical to \mathbf{W}^{-1} [35] and \mathbf{W}^* [69] is identical to \mathbf{W} [27].

The weighted SDS equations, using \mathbf{y} are

$$\mathbf{X}'[\text{Var}(\mathbf{Y})]^{-1}\mathbf{X}\sigma^2 = \mathbf{X}'[\text{Var}(\mathbf{Y})]^{-1}\mathbf{y}, \quad [71]$$

and the weighted SDS equations using \mathbf{y}^* are

$$\mathbf{X}^{*'}\mathbf{W}^{*-1}\mathbf{X}^*\sigma^2 = \mathbf{X}^{*'}\mathbf{W}^{*-1}\mathbf{y}^*. \quad [72]$$

The solutions to equations [71] and [72] are identical.

Now let

$$\mathbf{M}^* = \mathbf{I}_n - \mathbf{T}\mathbf{1}_n(\mathbf{1}_n'\mathbf{T}'\mathbf{T}\mathbf{1}_n)^{-1}\mathbf{1}_n'\mathbf{T}',$$

which after substituting [65] for $\mathbf{T}'\mathbf{T}$ is

$$\mathbf{I}_n - \mathbf{T}\mathbf{1}_n(\mathbf{1}_n'\mathbf{V}^{-1}\mathbf{1}_n)^{-1}\mathbf{1}_n'\mathbf{T}'. \quad [73]$$

By equality [37] the left hand side of weighted SDS equations using \mathbf{y}^* is

$$X^*W^{*-1}X^* = [\text{tr}(M^*TV_iT'M^*TV_jT')],$$

which after rotation of traces is

$$= [\text{tr}(T'M^*TV_iT'M^*TV_j)], \quad [74]$$

and since

$$\begin{aligned} T'M^*T &= T'(I_n - T1_n(1_n'V^{-1}1_n)^{-1}1_n'T')T, \\ &= T'T - T'T1_n(1_n'V^{-1}1_n)^{-1}1_n'T'T, \text{ or} \\ &= V^{-1} - V^{-1}1_n(1_n'V^{-1}1_n)^{-1}1_n'V^{-1} = P, \end{aligned} \quad [75]$$

then

$$X^*W^{*-1}X^* = [\text{tr}(PV_iPV_j)], \quad [76]$$

for $i, j = 1, 2, \dots, c+1$,

which is the left hand side of the equations used to estimate MIVQUE (Rao, 1971) for model [1]. Now by equality [39] the right hand side of the weighted SDS equations using y^* is

$$X^*W^{*-1}Y^* = [y'T'M^*TV_iT'M^*Ty],$$

which after substituting in [75] for $T'M^*T$ is

$$X^*W^{*-1}Y^* = [y'PV_iPy],$$

which is the right hand side of the MIVQUE equations (Rao, 1971). It has therefore been shown by these derivations that the weighting of the symmetric differences squared by the inverse of the total variance - covariance matrix to estimate the variance components yields estimates that are minimum variance unbiased estimates if the prior values used are near the true parameters. It must be emphasized that transformation of y to y^* was simply a device used to prove the above, which would not be recommended as a computational approach in practice.

COMPUTATIONAL REQUIREMENTS OF WSDS OR MIVQUE(0)

The computational requirements to complete analysis by MIVQUE(0) or WSDS will now be discussed. The left and right-hand side of the MIVQUE(0) or WSDS equations are as follows:

$$\begin{aligned}
 [\text{tr}(\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{V}_j)] = & \begin{vmatrix} \text{tr}(\mathbf{V}_1^2)\text{tr}(\mathbf{V}_1\mathbf{V}_2) & \dots & \text{tr}(\mathbf{V}_1\mathbf{V}_C) & \text{tr}(\mathbf{V}_1) \\ & \text{tr}(\mathbf{V}_2^2) & \dots & \text{tr}(\mathbf{V}_2\mathbf{V}_C) & \text{tr}(\mathbf{V}_2) \\ & & \ddots & \vdots & \vdots \\ \text{symmetric} & & & \text{tr}(\mathbf{V}_C^2) & \text{tr}(\mathbf{V}_C) \\ & & & & n. \end{vmatrix} \\
 - \frac{2}{n} & \begin{vmatrix} \mathbf{l}'_n\mathbf{V}_1^2\mathbf{l}_n & \mathbf{l}'_n\mathbf{V}_1\mathbf{V}_2\mathbf{l}_n & \dots & \mathbf{l}'_n\mathbf{V}_1\mathbf{V}_C\mathbf{l}_n & \mathbf{l}'_n\mathbf{V}_1\mathbf{l}_n \\ & \mathbf{l}'_n\mathbf{V}_2^2\mathbf{l}_n & \dots & \mathbf{l}'_n\mathbf{V}_2\mathbf{V}_C\mathbf{l}_n & \mathbf{l}'_n\mathbf{V}_2\mathbf{l}_n \\ & & \ddots & \vdots & \vdots \\ \text{symmetric} & & & \mathbf{l}'_n\mathbf{V}_C^2\mathbf{l}_n & \mathbf{l}'_n\mathbf{V}_C\mathbf{l}_n \\ & & & & n \end{vmatrix} \\
 + \frac{1}{n^2} & \begin{vmatrix} \mathbf{l}'_n\mathbf{V}_1\mathbf{l}_n \\ \mathbf{l}'_n\mathbf{V}_2\mathbf{l}_n \\ \vdots \\ \mathbf{l}'_n\mathbf{V}_C\mathbf{l}_n \\ n \end{vmatrix} [\mathbf{l}'_n\mathbf{V}_1\mathbf{l}_n \mathbf{l}'_n\mathbf{V}_2\mathbf{l}_n \dots \mathbf{l}'_n\mathbf{V}_C\mathbf{l}_n n] \quad [77]
 \end{aligned}$$

and

$$\begin{aligned}
 [\mathbf{y}'\mathbf{M}\mathbf{V}_i\mathbf{M}\mathbf{y}] = & [\mathbf{y}'\mathbf{V}_1\mathbf{y} \mathbf{y}'\mathbf{V}_2\mathbf{y} \dots \mathbf{y}'\mathbf{V}_C\mathbf{y} \mathbf{y}'\mathbf{y}]' \\
 & - 2\bar{\mathbf{y}}'[\mathbf{l}_n\mathbf{V}_1\mathbf{y} \mathbf{l}_n\mathbf{V}_2\mathbf{y} \dots \mathbf{l}_n\mathbf{V}_C\mathbf{y} n\bar{\mathbf{y}}]' \\
 & + \bar{\mathbf{y}}^2[\mathbf{l}_n\mathbf{V}_1\mathbf{l}_n \mathbf{l}_n\mathbf{V}_2\mathbf{l}_n \dots \mathbf{l}_n\mathbf{V}_C\mathbf{l}_n n]' \quad [78]
 \end{aligned}$$

The multiplications, additions, and storage needed to obtain and save the elements in the right hand sides of [77] and [78] are in table 1.

Table 1. Storage, multiplications and additions for each type of element required to set up the MIVQUE(0) or WSDS equations when relationship categories are not considered.

Type of element	Number of elements of this type ^a	Total multiplications for all elements of this type ^b	Total additions for all elements of this type
$\text{tr}(\mathbf{V}_i \mathbf{V}_j)$	$c(c+1)/2$	$n(n+1)c(c+1)/4$	$n(n+1)c(c+1)/4$
$\text{tr}(\mathbf{V}_i)$	c	0	nc
n	1	0	n
$\mathbf{l}'_n \mathbf{V}_i \mathbf{V}_j \mathbf{l}_n$	$c(c+1)/2$	$nc(c+1)/2$	$cn^2 + nc(c+1)/2$
$\mathbf{l}'_n \mathbf{V}_i \mathbf{l}_n$	c	0	$cn(n+1)/2$
$\mathbf{y}' \mathbf{V}_i \mathbf{y}$	c	$cn(n+1)/2$	$cn(n+1)/2$
$\mathbf{l}'_n \mathbf{V}_i \mathbf{y}$	c	nc	$n(n+1)c$
$\mathbf{y}' \mathbf{y}$	1	n	n
\bar{y}	1	1	n

^a c is the number of sets of random effects other than error

^b n is the total number of observations.

Computing $[\text{tr}(\mathbf{M}\mathbf{V}_i \mathbf{M}\mathbf{V}_j)]$ and $[\mathbf{y}' \mathbf{M}\mathbf{V}_i \mathbf{M}\mathbf{y}]$ from the elements in Table 1 and solving for the estimates of variance components also requires computer time and storage, but these requirements are small relative to the requirements needed to obtain the elements represented in Table 1. Additional computer resources are needed to compute and save \mathbf{V}_i matrices and store \mathbf{y} .

For animal breeding problems, the elements of \mathbf{V}_i are usually coefficients of relationship which specify the fraction of the i^{th} variance or covariance component's contribution to the covariance

between two members of y . The most widely used V_i matrix in animal breeding problems is Wright's numerator relationship matrix (A). If inbreeding has occurred, a strictly additive genetic model is usually invoked as an approximation because the nonadditive effects under inbreeding are difficult to interpret (Cockerham, 1954). If no inbreeding has occurred, nonadditive effects such as dominance and epistasis can also be considered. Maternal effects and covariance between direct and maternal effects can be important in animals. Matrices of dominance and epistatic coefficients of relationship can be constructed from Wright's numerator relationship matrix (A) if there is no inbreeding (Henderson, 1985). A can be saved for later use by storing only its p nonzero elements, where $p \leq n(n+1)/2$ and p is the number of nonzero elements in the upper triangle of A (Hudson et al., 1982). Three vectors of order n and one vector of order p in addition to the p vector containing the nonzero elements of A are needed to locate nonzero elements in A . This process can save considerable computer storage. Hudson et al. (1982) found that only 6 to 22.6% of the $n(n+1)/2$ upper triangular elements of A were nonzero for five breeds of dairy sires.

The multiplications required to complete WSDS or MIVQUE(0) equations can be reduced if the related pairs of individuals having records in y can be classified into a relatively small number of relationship categories. For example, with the mice data of Grimes and Harvey (1980), there were 107,398 related pairs of individuals distributed among only 39 relationship categories. Christian (1980) showed how to take advantage of these relationship categories to reduce

the computer time required to compute SDS by reducing the number of multiplications needed. It will now be shown how to reduce the number of multiplications required to do WSDS or MIVQUE(0) when there are a relatively small number of relationship categories.

If we can assume that no inbreeding has occurred, $\mathbf{x}_1 = \mathbf{1}_n \mathbf{1}'_{c+1}$ [17] can be substituted into [47] and [57] to obtain (after simplification)

$$\begin{aligned} \mathbf{x}'\mathbf{w}^{-1}\mathbf{x} = & (n-1)\mathbf{1}_{c+1}\mathbf{1}'_{c+1} - \frac{2}{n}\mathbf{x}'_2\mathbf{1}_q\mathbf{1}'_{c+1} - \frac{2}{n}\mathbf{1}_{c+1}\mathbf{1}'_q\mathbf{x}_2 \\ & + 2\mathbf{x}'_2\mathbf{x}_2 - \frac{2}{n}\mathbf{x}'_2\mathbf{H}\mathbf{H}'\mathbf{x}_2 + \frac{4}{n^2}\mathbf{x}_2\mathbf{1}_q\mathbf{1}'_q\mathbf{x}_2, \end{aligned} \quad [79]$$

and

$$\begin{aligned} \mathbf{x}'\mathbf{w}^{-1}\mathbf{y} = & (\mathbf{y}'\mathbf{y} - n\bar{y}^2)\mathbf{1}_{c+1} + 2\mathbf{x}'_2\mathbf{y}_2 - 2\bar{y}\mathbf{x}'_2\mathbf{h}_y \\ & + 2\bar{y}^2\mathbf{x}'_2\mathbf{1}_q \end{aligned} \quad [80]$$

for the left and right-hand sides of the WSDS equations. For purposes of comparison, it seems appropriate to give the SDS equations in this same notation. Substitute [17] into [43] and [54] to obtain

$$\begin{aligned} \mathbf{x}'\mathbf{x} = & 2n(n-1)\mathbf{1}_{c+1}\mathbf{1}'_{c+1} - 4\mathbf{x}'_2\mathbf{1}_q\mathbf{1}'_{c+1} - 4\mathbf{1}_{c+1}\mathbf{1}'_q\mathbf{x}_2 \\ & + 4\mathbf{x}'_2\mathbf{x}_2, \text{ and} \end{aligned} \quad [81]$$

$$\mathbf{x}'\mathbf{y} = 2n(\mathbf{y}'\mathbf{y} - n\bar{y}^2)\mathbf{1}_{c+1} - 2\mathbf{x}'_2\mathbf{H}\mathbf{y}_1 + 4\mathbf{x}'_2\mathbf{y}_2 \quad [82]$$

for the left and right hand sides of the SDS equations.

We can let

$$\mathbf{x}_2 = \mathbf{Z}\mathbf{U}, \quad [83]$$

where \mathbf{U} is an $r \times (c+1)$ matrix whose i^{th} column contains the coefficients for the i^{th} variance component among the r relationship categories, and \mathbf{Z} is a $q \times r$ matrix of zeros and ones that specifies the relationship category to which the pair of individuals belong whose

records are multiplied together to make an element of Y_2 .

We can also let

$$B = Z'Z, \quad [84]$$

where B is a diagonal matrix whose m^{th} diagonal element, for $m = 1, 2, \dots, r$, is the number of pairs of individuals related by the m^{th} relationship category. This is the same as the W matrix defined by Christian (1980).

Now we can let

$$N = H'Z, \quad [85]$$

or

$$N = \begin{bmatrix} n_{11} & n_{12} & \cdot & \cdot & \cdot & n_{1r} \\ n_{21} & n_{22} & \cdot & \cdot & \cdot & n_{2r} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ n_{n1} & n_{n2} & \cdot & \cdot & \cdot & n_{nr} \end{bmatrix}, \quad [86]$$

where n_{km} is the number of individuals in the entire sample related to individual k by the relationship of the m^{th} relationship category, for $k = 1, 2, \dots, n$, and $m = 1, 2, \dots, r$.

Hence,

$$N'N = \begin{bmatrix} \sum_k n_{k1}^2 & \sum_k n_{k1}n_{k2} & \cdot & \cdot & \cdot & \sum_k n_{k1}n_{kr} \\ \sum_k n_{k1}n_{k2} & \sum_k n_{k2}^2 & \cdot & \cdot & \cdot & \sum_k n_{k2}n_{kr} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \sum_k n_{k1}n_{kr} & \sum_k n_{k2}n_{kr} & \cdot & \cdot & \cdot & \sum_k n_{kr}^2 \end{bmatrix}. \quad [87]$$

We can let

$$Q = Z'1_q, \quad [88]$$

where Q is an $r \times 1$ vector whose i^{th} element is the same as the i^{th}

diagonal element of B. Substitute [83], [84], [85], and [88] into [79] and [80] to obtain

$$\begin{aligned} \mathbf{X}'\mathbf{W}^{-1}\mathbf{X} = & (n-1)\mathbf{1}_{C+1}\mathbf{1}'_{C+1} - \frac{2}{n}\mathbf{U}'\mathbf{Q}\mathbf{1}'_{C+1} - \frac{2}{n}\mathbf{1}_{C+1}\mathbf{Q}'\mathbf{U} \\ & + 2\mathbf{U}'\mathbf{B}\mathbf{U} - \frac{2}{n}\mathbf{U}'\mathbf{N}'\mathbf{N}\mathbf{U} + \frac{4}{n^2}\mathbf{U}'\mathbf{Q}\mathbf{Q}'\mathbf{U}, \end{aligned} \quad [89]$$

and

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y} = (\mathbf{y}'\mathbf{y} - n\bar{y}^2)\mathbf{1}_{C+1} + 2\mathbf{U}'\mathbf{Z}'\mathbf{Y}_2 - 2\bar{y}\mathbf{U}'\mathbf{N}'\mathbf{y} + 2\bar{y}^2\mathbf{U}'\mathbf{Q}, \quad [90]$$

for the left and right hand sides of the WSDS equations.

Likewise, substitute [83], [84], [85] and [88] into [81] and [82] to obtain

$$\mathbf{X}'\mathbf{X} = 2n(n-1)\mathbf{1}_{C+1}\mathbf{1}'_{C+1} - 4\mathbf{U}'\mathbf{Q}\mathbf{1}'_{C+1} - 4\mathbf{1}_{C+1}\mathbf{Q}'\mathbf{U} + 4\mathbf{U}'\mathbf{B}\mathbf{U}, \quad [91]$$

and

$$\mathbf{X}'\mathbf{Y} = 2n(\mathbf{y}'\mathbf{y} - n\bar{y}^2)\mathbf{1}_{C+1} - 2\mathbf{U}'\mathbf{N}'\mathbf{Y}_1 + 4\mathbf{U}'\mathbf{Z}'\mathbf{Y}_2, \quad [92]$$

for the left and right hand sides of the SDS equations. Matrices on the right hand side of [89], [90], [91] and [92] that can be stored economically are in table 2. Also in table 2 are the storage requirements for the matrices, and the number of multiplications and additions required to compute the matrices. It is assumed that square symmetric matrices will be half stored. Further computations required to obtain estimates of variance components by WSDS or SDS are small relative to the computations needed to construct some of the matrices in table 2, therefore, these are not given.

The r diagonal elements of B can be stored as Q so that B does not need to be stored separately. It is clear that estimates of variance components by SDS will take less time to compute than estimates of

variance components by WSDS because $\mathbf{N}'\mathbf{N}$ is needed for WSDS but not for SDS. A computational example for obtaining SDS and WSDS by [89] through [92] is presented in Appendix C.

Table 2. Multiplications, additions and storage needed to compute and save the matrices needed to set up the WSDS equations when relationship categories are considered.

Matrix	Storage ^{a,b}	Multiplications ^c	Additions
\mathbf{U}	rc	0	rc
\mathbf{Q}	r	0	$n(n-1)/2$
$\mathbf{N}'\mathbf{N}$	$r(r+1)/2$	$nr(r+1)/2$	$n^2+nr(r+1)/2$
$\mathbf{Z}'\mathbf{Y}_2$	r	$n(n-1)/2$	$n(n-1)/2$
$\mathbf{N}'\mathbf{y}$	r	nr	nr
$\mathbf{N}'\mathbf{Y}_1$	r	nr	nr
n	1	0	n
$\mathbf{y}'\mathbf{y}$	1	n	n
\bar{y}	1	1	n

^ar is the number of relationship categories.

^bc is the number of random effects other than residual.

^cn is the total number of observations.

The computational requirements for completing WSDS using the mice data of Grimes and Harvey (1980) will now be discussed. Arithmetic steps and storage required to compute WSDS by [89] and [90] and by [77] and [78] will be compared. For the mice data analyzed by Grimes and Harvey (1980), \mathbf{U} , \mathbf{Q} , r, c, n, and p are as follows:

$$u = \frac{1}{16}$$

[illegible]

Q = [4,739 10,215, 536 1,367 556 936 40 4,419 256 14,862 19,203 743 747
 1,280 304 621 302 6,323 264 56 107 176 4,603 2,546 9,214 127 821 56
 491 347 2,546 190 9,475 144 170 5,578 1,458 61 1,519]',

r = 39,

c = 4,

n = 1,780, and

p = 109,178.

The first three columns of U were obtained directly from the last three columns, excluding the first row, of table 5 of Grimes and Harvey (1980). The columns of U are the coefficients for the variance and covariance components for the covariances among individuals related by the relationship categories. The first column contains the coefficients for the direct additive genetic variance (σ_g^2), the second for maternal additive genetic variance (σ_{gm}^2), the third for direct-maternal additive covariance (σ_{ggm}), the fourth for permanent maternal environmental variance (σ_m^2), and the fifth for residual variance (σ_e^2). Q was obtained from the first column, excluding the first row, of Table 5 of Grimes and Harvey (1980).

The basic matrices needed to construct WSDS and SDS equations are given in table 3 with their storage requirements and the numbers of multiplications and additions required to obtain them for the mice data of Grimes and Harvey (1980).

A small amount of additional computer resources is needed to compute the WSDS or SDS equations from the matrices in table 3 and to solve for estimates of variance components.

A large amount of computer time and storage is needed to compute and store \mathbf{A} . Grimes and Harvey (1980) traced pedigrees back through 2 generations to compute \mathbf{A} . Assuming that their \mathbf{A} is essentially correct, the procedure of Hudson et al. (1982) would require storage for 223,696 numbers. In addition, computer time proportional to $n^2 = 3,168,400$ would be needed to compute \mathbf{A} . The elements of the other \mathbf{V}_i can be obtained from \mathbf{A} . In order to determine how much is gained by taking advantage of relationship categories by using [89] and [90], we need to evaluate computer requirements when we do not take advantage of relationship categories as in [77] and [78].

Table 3. Numbers of multiplications, additions and stored real numbers required to save matrices needed to set up WSDS and SDS equations for mice data of Grimes and Harvey (1980).

Matrix	Storage	Multiplications	Additions
\mathbf{U}	156	0	156
\mathbf{Q}	39	0	1,583,310
$\mathbf{N}'\mathbf{N}$	780	1,388,400	4,556,800
$\mathbf{Z}'\mathbf{Y}_2$	39	1,583,310	1,583,310
$\mathbf{N}'\mathbf{y}$	39	69,420	69,420
$\mathbf{N}'\mathbf{Y}_1$	39	69,420	69,420
\mathbf{n}	1	0	1,780
$\mathbf{y}'\mathbf{y}$	1	1,780	1,780
$\bar{\mathbf{y}}$	1	0	1,780

The storage, multiplications, and additions required to obtain the matrices needed for MIVQUE(0) or WSDS if we do not take advantage of relationship categories for the mice data of Grimes and Harvey (1980) are presented in table 4.

Table 4. Numbers of stored real numbers, multiplications, and additions required to compute each type of element needed to obtain the MIVQUE(0) or WSDS equations for the data of Grimes and Harvey (1980) if relationship categories are not considered.

Type of Element	Storage	Multiplications	Additions
$\text{tr}(\mathbf{V}_i \mathbf{V}_j)$	10	15,850,900	15,850,900
$\text{tr}(\mathbf{V}_i)$	4	0	7,120
n	1	0	1,780
$\mathbf{l}'_n \mathbf{V}_i \mathbf{V}_j \mathbf{l}_n$	10	17,800	12,691,400
$\mathbf{l}'_n \mathbf{V}_i \mathbf{l}_n$	4	1	6,340,360
$\mathbf{y}' \mathbf{V}_i \mathbf{y}$	4	6,340,360	6,340,360
$\mathbf{l}'_n \mathbf{V}_i \mathbf{y}$	4	7,120	12,680,720
$\mathbf{y}' \mathbf{y}$	1	1,780	1,780
\bar{y}	1	1	1,780

Comparison of tables 3 and 4 demonstrates that consideration of relationship categories increases the requirement for computer storage but reduces the requirement for multiplication and addition operations. Therefore, consideration of relationship categories by using expressions [89] and [90] instead of expressions [77] and [78] to set

up WSDS equations will reduce computer time required substantially and increase computer storage requirement slightly when the number of relationship categories is small. Computer resource requirements for obtaining A are the same whether or not relationship categories are considered.

METHODOLOGY

It was established in the current study that estimates of (co)variance components by SDS weighted by the inverse of the error variance-covariance matrix (WSDS) are MIVQUE if all (co)variances except σ_e^2 are near zero relative to σ_e^2 . Since SDS and WSDS are more computationally feasible than MIVQUE and REML under the animal model, it would be of interest to know how efficient SDS and WSDS estimates are relative to MIVQUE as σ_i^2/σ_e^2 departs from zero. Other approximate MIVQUE methods that reduce the computational requirements, or remove the arbitrariness of assigning priors without markedly reducing efficiency would also be of interest. Permanent maternal environmental effects (variance = σ_m^2) will usually account for a portion of the phenotypic variance of measurements taken on young animals. MIVQUE with all priors set to zero except σ_m^2 , and σ_e^2 (MIVQUE (0, M, E)) is easier to compute than MIVQUE because the $\text{Var}(\mathbf{y})$ under the assumption that all variances except σ_m^2 and σ_e^2 are zero can be easily inverted using partitioned matrix techniques (Henderson and Searle, 1981). To avoid the arbitrariness of assigning prior values, Rao (1971) recommended assigning priors: $\sigma_i^2 = 1$, for all i , and $\sigma_e^2 = 1$. This method will be referred to in this paper as unweighted MIVQUE or MIVQUE(1).

A numerical study was conducted to evaluate the influence of the unknown (co)variances on the efficiency of SDS, WSDS, MIVQUE (0, M, E),

and MIVQUE(1) relative to MIVQUE (true parameters used as priors) under the animal model.

Two mating designs (Figure 1) described by Thompson (1976) and three mating designs described by Eisen (1967) (figure 2) were chosen for this evaluation. Thompson's (1976) designs were chosen because they are appropriate for species with one or two offspring, whereas Eisen's (1967) designs were chosen because they are appropriate for litter bearing species. For the Thompson designs, a random sire (S) is mated to two random dams (D_1 and D_2) to produce a male and a female offspring from each mating. In design A, a female progeny from one dam and a male progeny from the other dam are bred to random mates (M_1 and M_2) to produce two progeny each. In design B, the female progeny from both dams are bred to random males to produce two progeny each. This results in eight progeny to form a set of a Thompson design.

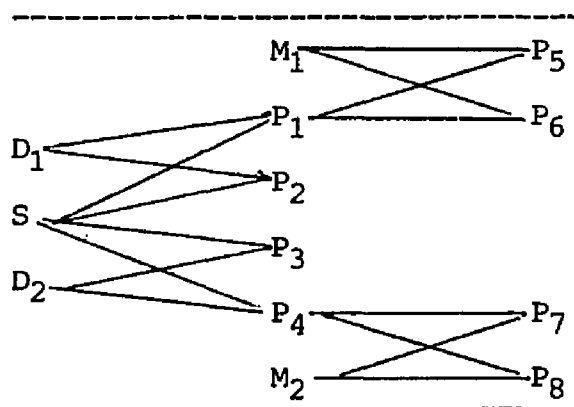


Figure 1. Two mating designs of Thompson (1976). In design A, P_1 and P_3 are males and P_2 and P_4 are females. In design B, P_2 and P_3 are males and P_1 and P_4 are females.

For the Eisen designs, s sets are sampled from initial random matings. The 18 individuals that comprise a set are shown in figure 2. S_1 and S_2 are male parents, D_1, D_2, \dots, D_8 are female parents, and O_1, O_2, \dots, O_8 are offspring. Each set contains three unrelated families. In design I, S_1 and S_2 are a full sib family, D_1, D_2, D_3 and D_4 are a full-sib family, and D_5, D_6, D_7 , and D_8 are a half sib family. In design II, S_1, D_1 , and D_2 are a full sib family; S_2, D_3 , and D_4 are a full-sib family; and D_5, D_6, D_7 , and D_8 are a full sib family. Design III is the same as design II with the exception that D_5, D_6, D_7 , and D_8 are a half-sib family instead of a full-sib family.

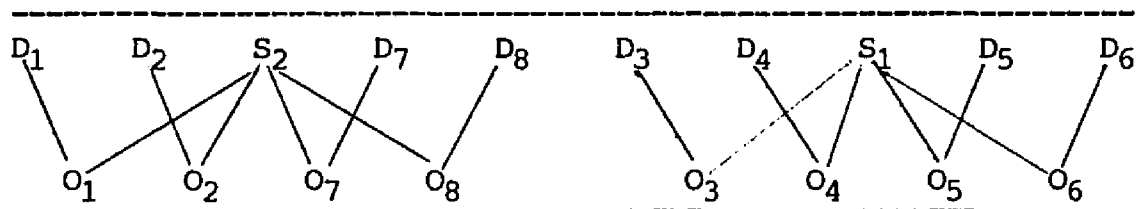


Figure 2. The 18 individuals comprising a set of an Eisen (1967) design. S_1 and S_2 are male parents, D_1, D_2, \dots, D_8 are female parents, and O_1, O_2, \dots, O_8 are offspring.

The model assumed in this study for the phenotype of the i^{th} individual from the j^{th} dam is

$$y_{ij} = \mu + g_i + g_j^m + m_j + e_{ij}, \quad [93]$$

where μ is a fixed unknown constant,

g_i is the direct genic effect of the i^{th} individual,

g_j^m is the maternal genic effect of the j^{th} dam,

m_j is the permanent maternal environmental effect of the j^{th} dam,

and

e_{ij} is the temporary environmental effect,

$$E(e_{ij}) = E(m_j) = E(g_j^m) = E(g_i) = 0,$$

$$\text{Var}(g_i) = \sigma_g^2, \text{Var}(g_j^m) = \sigma_{gm}^2, \text{Var}(m_j) = \sigma_m^2, \text{Cov}(g_i, g_i^m) = \sigma_{ggm} \text{ and} \\ \text{Var}(e_{ijk}) = \sigma_e^2, \text{ and}$$

$$\text{Cov}(g_j, m_j) = \text{Cov}(e_i, e_{ij}) = \text{Cov}(g_j^m, m_j) = \text{Cov}(m_j, e_{ij}) = \text{Cov}(g_j^m, e_{ij}) = 0$$

Since individuals of different sets are unrelated, it is convenient to define the variance of terms in the formulas for sampling variance as a function of the number of sets (s). Let y be the vector of phenotypes for one set. The variance of y can be written

$$\text{Var}(y) = V = V_1 \sigma_g^2 + V_2 \sigma_{ggm} + V_3 \sigma_{gm}^2 + V_4 \sigma_m^2 + I_n \sigma_e^2, \quad [94]$$

where n is the number of individuals in a set ($n = 8$ for Thompson designs, $n = 18$ for Eisen designs); and V_1 , V_2 , V_3 , and V_4 are $n \times n$ matrices of coefficients which when multiplied by σ_g^2 , σ_{ggm} , σ_{gm}^2 , and σ_m^2 specify the contribution of σ_g^2 , σ_{ggm} , σ_{gm}^2 , and σ_m^2 to the variance among individuals in a set. V_1 , V_2 , V_3 , and V_4 for the Eisen and Thompson designs are in Appendix B for the individuals in a set. The coefficients in V_i , for $i = 1, 2, \dots, 4$, were obtained from table 1 of Thompson (1976) and table 1 of Eisen (1967). For the V_i matrixes in Appendix B, y was sorted for the Thompson designs as P_1, P_2, \dots, P_8 (figure 1) and for the Eisen designs as $S_1, S_2, D_1, D_2, \dots, D_8, O_1, O_2, \dots, O_8$ (Figure 2).

Relative efficiency in this study was computed as:

$$\text{Relative Efficiency} = \frac{\text{Var}(\hat{\sigma}_1^2)}{\text{Var}(\hat{\sigma}_1^2)}, \quad [95]$$

where $\hat{\sigma}_1^2$ is an SDS, WSDS, MIVQUE (0, M, E), or MIVQUE(1) estimate of the i^{th} variance component and $\hat{\sigma}_1^2$ is the MIVQUE estimate of the i^{th} variance component.

The sampling variances of \hat{g}^2 and \dot{g}^2 can be written as a function of the number of sets (s) and the V_i matrices defined previously. The sampling variance among MIVQUE estimates of the variance components for data resulting from s sets is

$$\begin{aligned} \text{Var}(\dot{g}^2) = & 2\{s[\text{tr}(V^{-1}V_iV^{-1}V_j)] - 2(1_n'V^{-1}1_n)^{-1}[1_n'V^{-1}V_iV^{-1}V_jV^{-1}1_n] \\ & + (1_n'V^{-1}1_n)^{-2}[1_n'V^{-1}V_iV^{-1}1_n][1_n'V^{-1}V_jV^{-1}1_n]\}^{-1} \end{aligned} \quad [96]$$

for $i, j = 1, 2, \dots, 5$, where

$$V_5 = I_n.$$

The sampling variance among SDS estimates of (co)variance components is

$$\text{Var}(\hat{g}^2) = (X'X)^{-1} \text{Var}(X'Y) (X'X)^{-1}, \quad [97]$$

where for s sets

$$\begin{aligned} \text{Var}(X'Y) = & 8s\{s[\text{sn}^2\text{tr}(V^2) - 2n1_n'V^21_n + (1_n'V1_n)^2]1_{c+1}'1_{c+1} \\ & - \text{sn}\{[\text{tr}(F_iV^2)]1_{c+1}' + 1_{c+1}[\text{tr}(F_jV^2)]\} \\ & + \text{sn}\{[\text{tr}(V_iV^2)]1_{c+1}' + 1_{c+1}[\text{tr}(V_jV^2)]\} \\ & + [1_n'VF_iV1_n]1_{c+1}' + 1_{c+1}[1_n'VF_jV1_n] \\ & - [1_n'VW_iV1_n]1_{c+1}' - 1_{c+1}[1_n'VW_jV1_n] \\ & + [\text{tr}(F_iVF_jV)] \\ & - [\text{tr}(F_iVW_jV)] - [\text{tr}(V_iVF_jV)] \\ & + [\text{tr}(V_iVW_jV)]\}, \end{aligned} \quad [98]$$

where

$$F_i = \begin{vmatrix} \sum_1 (v_{11})_i & 0 & 0 & \dots & 0 \\ 0 & \sum_1 (v_{21})_i & 0 & \dots & 0 \\ 0 & 0 & \cdot & & \cdot \\ \vdots & \vdots & & \cdot & \vdots \\ \vdots & \vdots & & & \cdot \\ 0 & 0 & \dots & \sum_1 (v_{n1})_i & \end{vmatrix}, \quad [99]$$

for $l = 1, 2, \dots, n$, and

$$\mathbf{X}'\mathbf{X} = 2s\{sn^2\mathbf{1}_{C+1}\mathbf{1}_{C+1}' - [\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n]\mathbf{1}_{C+1}' - \mathbf{1}_{C+1}[\mathbf{1}_n'\mathbf{V}_j\mathbf{1}_n] + [\text{tr}(\mathbf{V}_i\mathbf{V}_j)]\}. \quad [100]$$

The sampling variance among WSDS estimates of (co)variance components is

$$\text{Var}(\hat{\sigma}^2) = (\mathbf{X}'\mathbf{W}^{-1}\mathbf{X})^{-1} \text{Var}(\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y}) (\mathbf{X}'\mathbf{W}^{-1}\mathbf{X})^{-1}, \quad [101]$$

where for s sets

$$\begin{aligned} \text{Var}(\mathbf{X}'\mathbf{W}^{-1}\mathbf{Y}) &= 2\{s[\text{tr}(\mathbf{W}\mathbf{V}_i\mathbf{W}\mathbf{V}_j)] - \frac{4}{n} [\mathbf{1}_n'\mathbf{W}\mathbf{V}_i\mathbf{W}\mathbf{V}_j\mathbf{1}_n] \\ &\quad + \frac{1}{n^2} \{2 [\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_j\mathbf{W}\mathbf{V}_i\mathbf{1}_n] + 2[\mathbf{1}_n'\mathbf{W}\mathbf{V}_i\mathbf{1}_n][\mathbf{1}_n'\mathbf{W}\mathbf{V}_j\mathbf{1}_n] \\ &\quad + [\mathbf{1}_n'\mathbf{W}\mathbf{V}_i\mathbf{V}_i\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_j\mathbf{1}_n] + [\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n][\mathbf{1}_n'\mathbf{W}\mathbf{V}_j\mathbf{V}_j\mathbf{1}_n] \\ &\quad - \frac{2}{n^3} [\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n\{[\mathbf{1}_n'\mathbf{W}\mathbf{V}_i\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_j\mathbf{1}_n] + [\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n][\mathbf{1}_n'\mathbf{W}\mathbf{V}_j\mathbf{1}_n]\} \\ &\quad + \frac{1}{n^4} (\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n)^2[\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_j\mathbf{1}_n]\}, \end{aligned} \quad [102]$$

and

$$\mathbf{X}'\mathbf{W}^{-1}\mathbf{X} = s[\text{tr}(\mathbf{V}_i\mathbf{V}_j)] - \frac{2}{n} [\mathbf{1}_n'\mathbf{V}_i\mathbf{V}_j\mathbf{1}_n] + \frac{1}{n^2} [\mathbf{1}_n'\mathbf{V}_i\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_j\mathbf{1}_n]. \quad [103]$$

The sampling variance among MIVQUE (0, M, E) or MIVQUE(1) estimates of (co)variance components is as follows:

$$\text{Var}(\hat{\sigma}^2) = (\text{LHS})^{-1} \text{Var}(\text{RHS}) (\text{LHS})^{-1}, \quad [104]$$

where

$$\hat{\sigma}^2 = (\text{LHS})^{-1}\text{RHS}. \quad [105]$$

For s sets,

$$\begin{aligned}
 \text{Var(RHS)} = & 2\{s[\text{tr}(\mathbf{G}\mathbf{V}_i\mathbf{G}\mathbf{V}_j)] \\
 & - 2(\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{1}_n)^{-1}\{[\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{G}\mathbf{V}_i\mathbf{G}\mathbf{1}_n] + [\mathbf{1}_n'\mathbf{G}\mathbf{V}_j\mathbf{G}\mathbf{V}_i\mathbf{V}_a^{-1}\mathbf{1}_n]\} \\
 & + (\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{1}_n)^{-2}\{2[\mathbf{1}_n'\mathbf{G}\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{G}\mathbf{V}_i\mathbf{V}_a^{-1}\mathbf{1}_n] \\
 & + 2[\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_i\mathbf{G}\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{G}\mathbf{1}_n] \\
 & + [\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_i\mathbf{V}_a^{-1}\mathbf{1}_n][\mathbf{1}_n'\mathbf{G}\mathbf{V}_j\mathbf{G}\mathbf{1}_n] \\
 & + [\mathbf{1}_n'\mathbf{G}\mathbf{V}_i\mathbf{G}\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{V}_a^{-1}\mathbf{1}_n]\} \\
 & - 2(\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{1}_n)^{-3}(\mathbf{1}_n'\mathbf{G}\mathbf{1}_n)\{[\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_i\mathbf{V}_a^{-1}\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{G}\mathbf{1}_n] \\
 & + [\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_i\mathbf{G}\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{V}_a^{-1}\mathbf{1}_n]\} \\
 & + (\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{1}_n)^{-4}(\mathbf{1}_n'\mathbf{G}\mathbf{1}_n)^2[\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_i\mathbf{V}_a^{-1}\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{V}_a^{-1}\mathbf{1}_n]\}, \quad [106]
 \end{aligned}$$

where

$$\begin{aligned}
 \mathbf{V}_a &= \sigma_m^2\mathbf{V}_4 + \sigma_e^2\mathbf{I}_n, \text{ for MIVQUE (0, M, E), and} \\
 \mathbf{V}_a &= \mathbf{V}_1 + \mathbf{V}_2 + \mathbf{V}_3 + \mathbf{V}_4 + \mathbf{I}_n, \text{ for MIVQUE(1), and} \\
 \mathbf{G} &= \mathbf{V}_a^{-1}\mathbf{W}\mathbf{V}_a^{-1}; \text{ and} \\
 \text{LHS} &= s[\text{tr}(\mathbf{V}_a^{-1}\mathbf{v}_i\mathbf{V}_a^{-1}\mathbf{v}_j)] \\
 &\quad - 2(\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{1}_n)^{-1}[\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_i\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{V}_a^{-1}\mathbf{1}_n] \\
 &\quad + (\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{1}_n)^{-2}[\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_i\mathbf{V}_a^{-1}\mathbf{1}_n][\mathbf{1}_n'\mathbf{V}_a^{-1}\mathbf{v}_j\mathbf{V}_a^{-1}\mathbf{1}_n]. \quad [107]
 \end{aligned}$$

Two hundred sets were considered resulting in 1,600 individuals for Thompson (1976) designs and 3,600 individuals for Eisen designs.

Each parameter other than the error variance was set to two levels - direct genic at 15 or 30, maternal genic at 15 or 30, correlation between direct and maternal genic at -.1 or -.3, and permanent maternal environment at 20 or 50. The phenotypic variance was held constant at 100. Taking all possible combinations of the four parameters at two levels each results in 16 parameter set combinations. The error variance was computed as the difference between 100 and the sum of all

other components. However, for the parameter set in which $\sigma_g^2 = 30$, $\sigma_{gm}^2 = 30$, $\sigma_{ggm} = -.1$, and $\sigma_m^2 = 50$, the sum of these components is 104 > 100. Therefore, for this set, $\sigma_g^2 = 27.8$, $\sigma_{gm}^2 = 27.8$, $\sigma_{ggm} = -.1$, $\sigma_m^2 = 46.3$, and $\sigma_e^2 = 3.70$ to hold the phenotypic variance constant and to keep σ_e^2 positive. In addition, the parameter set $\sigma_g^2 = 9.8$, $\sigma_{gm}^2 = 9.8$, $\sigma_{ggm} = -1.96$, and $\sigma_e^2 = 21.56$ was used to make a direct comparison of this numerical procedure with the simulation study of Grimes and Harvey (1980).

RESULTS AND DISCUSSION

Standard errors of SDS estimates of (co)variance components computed as the square root of the result of [97] agree quite well with the standard errors obtained in the simulation study of Grimes and Harvey (1980) (table 5).

Table 5. Comparison of standard errors of SDS estimates of variance components obtained by simulation study of Grimes and Harvey (1980) for a maternal effects model with standard errors obtained by the numerical method of the present study.

Item	Mating ^a Design	Parameters ^b				
		σ_g^2	σ_{ggm}	σ_{gm}^2	σ_m^2	σ_e^2
----- Parameter values -----						
Parameter values		9.8	-1.96	9.8	9.8	21.56
----- Standard errors -----						
Current study	A	9.3	9.2	15.9	9.8	5.1
Grimes and Harvey (1980)		9.4	10.1	17.1	10.3	5.0
Current study	B	12.1	6.2	7.9	4.9	6.2
Grimes and Harvey (1980)		12.8	6.8	7.9	5.0	6.4

^a The mating designs were due to Thompson (1976), of which 200 replicates were used.

^b σ_g^2 , σ_{gm}^2 , σ_m^2 , and σ_e^2 are variances due to direct genic, maternal genic, permanent maternal environmental, and environmental effects, and σ_{ggm} is the covariance between direct and maternal genic effects.

The efficiencies [95] of SDS and WSDS estimates of (co)variance components relative to MIVQUE are in tables 6 and 7. In tables 6, and 7, the efficiencies corresponding to each parameter set are ranked by σ_e^2 from high to low. Efficiency of SDS and WSDS relative to MIVQUE seems to follow for the most part the same ranking as σ_e^2 (table 6 and

7). This result is to be expected for the relative efficiency of WSDS because the assumptions underlying the MIVQUE(0) property of WSDS are violated to a greater and greater extent as σ_e^2 becomes smaller. This is because σ_i^2 / σ_e^2 increases as σ_e^2 decreases in this study. Discrepancies between the rankings of efficiency of WSDS and σ_e^2 are due to certain combinations of parameters having more effect on efficiency than other combinations. The efficiencies of SDS and WSDS relative to MIVQUE were quite sensitive to decreases in σ_e^2 for all designs except Thompson B. For the Thompson B design, efficiency of SDS and WSDS varied little over all parameter sets studied. Comparison of tables 6 and 7 showed that WSDS is more efficient than SDS for almost all parameter sets, estimates of variance components, and mating designs. Exceptions to this result occur when σ_m^2 is estimated from Eisen designs I, II, and III or when σ_e^2 is estimated from Eisen design III.

Table 6. Efficiency^a of SDS estimates of (co)variance components relative to MIVQUE estimates computed from mating designs of Thompson^b and Eisen^b replicated 200 times each.

Rank ^d	Parameters ^c					Efficiency of				
	σ_e^2	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Thompson A Design										
1	59.00	15	15	-.3	20	.66	.67	.68	.71	.66
2	53.00	15	15	-.1	20	.66	.66	.68	.72	.66
3	47.72	15	30	-.3	20	.65	.64	.66	.71	.64
3	47.72	30	15	-.3	20	.68	.67	.68	.72	.67
5	39.24	15	30	-.1	20	.65	.63	.66	.71	.63
5	39.24	30	15	-.1	20	.67	.66	.68	.72	.65
7	38.00	30	30	-.3	20	.66	.64	.66	.71	.64
8	29.00	15	15	-.3	50	.62	.58	.61	.68	.59
9	26.00	30	30	-.1	20	.65	.62	.65	.71	.62
10	23.00	15	15	-.1	50	.60	.55	.60	.67	.57
11	17.72	15	30	-.3	50	.57	.50	.56	.65	.54
11	17.72	30	15	-.3	50	.61	.56	.60	.68	.58
13	9.24	15	30	-.1	50	.51	.44	.52	.63	.48
13	9.24	30	15	-.1	50	.57	.51	.57	.66	.54
15	8.00	30	30	-.3	50	.56	.49	.55	.65	.52
16	3.70	27.8	27.8	-.1	46.3	.52	.45	.53	.64	.49
Thompson B Design										
1	59.00	15	15	-.3	20	.80	.89	.88	.95	.82
2	53.00	15	15	-.1	20	.80	.90	.89	.95	.81
3	47.72	15	30	-.3	20	.80	.89	.89	.95	.81
3	47.72	30	15	-.3	20	.82	.91	.88	.94	.83
5	39.24	15	30	-.1	20	.80	.90	.89	.95	.80
5	39.24	30	15	-.1	20	.82	.91	.89	.94	.82
7	38.00	30	30	-.3	20	.82	.91	.89	.95	.83
8	29.00	15	15	-.3	50	.82	.88	.82	.93	.83
9	26.00	30	30	-.1	20	.80	.91	.89	.95	.80
10	23.00	15	15	-.1	50	.82	.89	.81	.93	.82
11	17.72	15	30	-.3	50	.82	.88	.80	.93	.82
11	17.72	30	15	-.3	50	.84	.90	.81	.93	.84
13	9.24	15	30	-.1	50	.81	.88	.77	.93	.81
13	9.24	30	15	-.1	50	.83	.90	.80	.93	.83
15	8.00	30	30	-.3	50	.83	.89	.79	.93	.83
16	3.70	27.8	27.8	-.1	46.3	.81	.90	.79	.93	.81

Table 6 continued

Rank ^d	Parameters ^c					Efficiency of				
	σ_e^2	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Eisen I Design										
1	59.00	15	15	-.3	20	.53	.72	.61	.67	.65
2	53.00	15	15	-.1	20	.53	.71	.62	.67	.62
3	47.72	15	30	-.3	20	.51	.71	.64	.69	.57
3	47.72	30	15	-.3	20	.56	.72	.62	.67	.63
5	39.24	15	30	-.1	20	.49	.69	.64	.69	.53
5	39.24	30	15	-.1	20	.55	.71	.62	.67	.58
7	38.00	30	30	-.3	20	.53	.71	.64	.68	.55
8	29.00	15	15	-.3	15	.46	.64	.56	.64	.46
9	26.00	30	30	-.1	20	.49	.68	.64	.67	.48
10	23.00	15	15	-.1	50	.44	.62	.56	.64	.42
11	17.72	15	30	-.3	50	.40	.58	.55	.63	.37
11	17.72	30	15	-.3	50	.46	.63	.56	.63	.43
13	9.24	15	30	-.1	50	.35	.52	.54	.62	.31
13	9.24	30	15	-.1	50	.42	.58	.56	.63	.37
15	8.00	30	30	-.3	50	.40	.56	.55	.62	.35
16	3.70	27.8	27.8	-.1	46.3	.36	.53	.55	.62	.30
Eisen II Design										
1	59.00	15	15	-.3	20	.62	.76	.72	.75	.67
2	53.00	15	15	-.1	20	.61	.76	.73	.76	.64
3	47.72	15	30	-.3	20	.59	.74	.72	.78	.60
3	47.72	30	15	-.3	20	.66	.78	.72	.75	.66
5	39.24	15	30	-.1	20	.56	.73	.73	.79	.56
5	39.24	30	15	-.1	20	.64	.78	.72	.76	.62
7	38.00	30	30	-.3	20	.62	.75	.72	.78	.60
8	29.00	15	15	-.3	50	.54	.69	.66	.79	.50
9	26.00	30	30	-.1	20	.58	.74	.72	.78	.54
10	23.00	15	15	-.1	50	.51	.67	.66	.80	.47
11	17.72	15	30	-.3	50	.47	.62	.65	.80	.42
11	17.72	30	15	-.3	50	.55	.69	.66	.78	.50
13	9.24	15	30	-.1	50	.41	.57	.65	.81	.36
13	9.24	30	15	-.1	50	.50	.66	.65	.79	.44
15	8.00	30	30	-.3	50	.48	.62	.64	.79	.42
16	3.70	27.8	27.8	-.1	46.3	.44	.59	.65	.80	.37

Table 6 continued

Rank ^d	Parameters ^c					Efficiency of				
	σ_e^2	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Eisen III Design										
1	59.00	15	15	-.3	20	.67	.87	.90	.91	.71
2	53.00	15	15	-.1	20	.66	.87	.89	.91	.72
3	47.72	15	30	-.3	20	.65	.85	.87	.91	.66
3	47.72	30	15	-.3	20	.70	.88	.88	.90	.70
5	39.24	15	30	-.1	20	.63	.84	.85	.89	.62
5	39.24	30	15	-.1	20	.68	.87	.86	.88	.66
7	38.00	30	30	-.3	20	.67	.84	.84	.89	.65
8	29.00	15	15	-.3	50	.61	.83	.85	.89	.57
9	26.00	30	30	-.1	20	.63	.82	.81	.85	.58
10	23.00	15	15	-.1	50	.59	.82	.83	.88	.53
11	17.72	15	30	-.3	50	.56	.76	.78	.85	.48
11	17.72	30	15	-.3	50	.62	.83	.81	.86	.54
13	9.24	15	30	-.1	50	.50	.72	.74	.82	.41
13	9.24	30	15	-.1	50	.57	.80	.77	.83	.48
15	8.00	30	30	-.3	50	.56	.75	.75	.82	.46
16	3.70	27.8	27.8	-.1	46.3	.51	.72	.73	.80	.41

^a Efficiency is the standard error of the MIVQUE estimate of (co)variance component divided by the standard error of the SDS estimate.

^b Mating designs are defined in the text.

^c Parameters are defined as follows: σ_g^2 , σ_{gm}^2 , σ_m^2 , and σ_e^2 are variances due to direct additive genetic, maternal additive genetic, permanent maternal environmental, and residual error effects; and r_{ggm} and σ_{ggm} are the correlation and covariance between direct and maternal additive genetic effects.

^d Parameter sets are ranked by σ_e^2 , from high to low.

Table 7. Efficiency^a of WSDS estimates of (co)variance components relative to MIVQUE estimates computed from mating designs of Thompson^b and Eisen^b replicated 200 times each.

Rank ^d	Parameters ^c					Efficiency of				
	σ_e^2	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Thompson A Design										
1	59.00	15	15	-.3	20	.96	.95	.95	.97	.97
2	53.00	15	15	-.1	20	.96	.93	.94	.95	.96
3	47.72	15	30	-.3	20	.94	.91	.91	.94	.95
3	47.72	30	15	-.3	20	.93	.92	.93	.95	.94
5	39.24	15	30	-.1	20	.92	.89	.89	.91	.93
5	39.24	30	15	-.1	20	.92	.90	.91	.93	.92
7	38.00	30	30	-.3	20	.91	.89	.90	.93	.92
8	29.00	15	15	-.3	50	.87	.80	.83	.89	.87
9	26.00	30	30	-.1	20	.88	.84	.85	.89	.88
10	23.00	15	15	-.1	50	.84	.76	.80	.87	.85
11	17.72	15	30	-.3	50	.80	.70	.75	.84	.80
11	17.72	30	15	-.3	50	.83	.75	.80	.87	.83
13	9.24	15	30	-.1	50	.72	.61	.69	.80	.72
13	9.24	30	15	-.1	50	.76	.69	.75	.84	.77
15	8.00	30	30	-.3	50	.76	.67	.73	.83	.76
16	3.70	27.8	27.8	-.1	46.3	.71	.62	.69	.80	.71
Thompson B Design										
1	59.00	15	15	-.3	20	.99	.99	.97	.99	.99
2	53.00	15	15	-.1	20	.98	.99	.97	.99	.98
3	47.72	15	30	-.3	20	.97	.99	.96	.99	.97
3	47.72	30	15	-.3	20	.97	.98	.97	.99	.97
5	39.24	15	30	-.1	20	.96	.99	.95	.98	.96
5	39.24	30	15	-.1	20	.96	.98	.97	.99	.96
7	38.00	30	30	-.3	20	.96	.98	.96	.98	.96
8	29.00	15	15	-.3	50	.99	.95	.87	.96	.99
9	26.00	30	30	-.1	20	.93	.98	.95	.98	.93
10	23.00	15	15	-.1	50	.98	.96	.86	.95	.98
11	17.72	15	30	-.3	50	.98	.95	.83	.95	.98
11	17.72	30	15	-.3	50	.98	.95	.87	.96	.98
13	9.24	15	30	-.1	50	.96	.95	.80	.95	.96
13	9.24	30	15	-.1	50	.96	.95	.85	.95	.96
15	8.00	30	30	-.3	50	.97	.95	.83	.95	.97
16	3.70	27.8	27.8	-.1	46.3	.95	.95	.82	.95	.95

Table 7 continued

Rank ^d	Parameters ^c					Efficiency of				
	σ_e^2	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Eisen I Design										
1	59.00	15	15	-.3	20	.92	.94	.92	.82	.80
2	53.00	15	15	-.1	20	.90	.93	.90	.80	.76
3	47.72	15	30	-.3	20	.87	.89	.85	.74	.68
3	47.72	30	15	-.3	20	.87	.90	.87	.78	.75
5	39.24	15	30	-.1	20	.82	.86	.80	.69	.62
5	39.24	30	15	-.1	20	.82	.88	.83	.74	.69
7	38.00	30	30	-.3	20	.82	.85	.81	.70	.65
8	29.00	15	15	-.3	15	.84	.86	.85	.64	.52
9	26.00	30	30	-.1	20	.74	.80	.74	.63	.55
10	23.00	15	15	-.1	50	.80	.83	.82	.61	.47
11	17.72	15	30	-.3	50	.74	.75	.75	.56	.41
11	17.72	30	15	-.3	50	.76	.80	.80	.60	.48
13	9.24	15	30	-.1	50	.64	.67	.69	.53	.34
13	9.24	30	15	-.1	50	.68	.74	.75	.56	.40
15	8.00	30	30	-.3	50	.66	.69	.71	.54	.38
16	3.70	27.8	27.8	-.1	46.3	.59	.64	.68	.52	.33
Eisen II Design										
1	59.00	15	15	-.3	20	.94	.95	.94	.88	.91
2	53.00	15	15	-.1	20	.91	.94	.92	.86	.88
3	47.72	15	30	-.3	20	.88	.90	.88	.80	.84
3	47.72	30	15	-.3	20	.90	.93	.90	.83	.88
5	39.24	15	30	-.1	20	.84	.88	.86	.78	.79
5	39.24	30	15	-.1	20	.86	.91	.88	.80	.84
7	38.00	30	30	-.3	20	.86	.88	.85	.77	.82
8	29.00	15	15	-.3	50	.83	.85	.87	.76	.71
9	26.00	30	30	-.1	20	.79	.84	.82	.73	.74
10	23.00	15	15	-.1	50	.79	.82	.85	.74	.67
11	17.72	15	30	-.3	50	.73	.74	.80	.69	.61
11	17.72	30	15	-.3	50	.79	.81	.84	.72	.68
13	9.24	15	30	-.1	50	.64	.67	.77	.67	.52
13	9.24	30	15	-.1	50	.71	.76	.80	.69	.61
15	8.00	30	30	-.3	50	.69	.71	.78	.67	.59
16	3.70	27.8	27.8	-.1	46.3	.63	.67	.76	.66	.53

Table 7 continued

Rank ^d	Parameters ^c					Efficiency of				
	σ_e^2	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Eisen III Design										
1	59.00	15	15	-.3	20	.95	.97	.95	.87	.83
2	53.00	15	15	-.1	20	.93	.97	.94	.85	.80
3	47.72	15	30	-.3	20	.91	.94	.90	.80	.74
3	47.72	30	15	-.3	20	.92	.95	.93	.82	.78
5	39.24	15	30	-.1	20	.88	.92	.87	.77	.67
5	39.24	30	15	-.1	20	.89	.94	.90	.79	.72
7	38.00	30	30	-.3	20	.89	.92	.88	.76	.70
8	29.00	15	15	-.3	15	.86	.91	.88	.72	.58
9	26.00	30	30	-.1	20	.83	.89	.84	.70	.60
10	23.00	15	15	-.1	50	.83	.89	.87	.70	.53
11	17.72	15	30	-.3	50	.78	.83	.80	.65	.48
11	17.72	30	15	-.3	50	.82	.88	.85	.68	.53
13	9.24	15	30	-.1	50	.69	.77	.76	.61	.40
13	9.24	30	15	-.1	50	.76	.85	.81	.63	.46
15	8.00	30	30	-.3	50	.74	.80	.77	.61	.45
16	3.70	27.8	27.8	-.1	46.3	.68	.77	.75	.59	.40

^a Efficiency is the standard error of the MIVQUE estimate of (co)variance component divided by the standard error of the WSDS estimate.

^b Mating designs are defined in the text.

^c Parameters are defined as follows: σ_g^2 , σ_{gm}^2 , σ_m^2 , and σ_e^2 are variances due to direct additive genetic, maternal additive genetic, permanent maternal environmental, and residual error effects; and r_{ggm} and σ_{ggm} are the correlation and covariance between direct and maternal additive genetic effects.

^d Parameter sets are ranked by σ_e^2 , from high to low.

The efficiencies of MIVQUE (0, M, E) estimates of (co)variance components relative to MIVQUE are in table 8. In table 8, efficiencies corresponding to each parameter set are ranked by $\sigma_m^2 + \sigma_e^2$ from high to low. The efficiency of MIVQUE (0, M, E) appears to follow the same ranking with some exceptions as $\sigma_m^2 + \sigma_e^2$ (table 8). Unlike SDS and WSDS, the efficiency of MIVQUE (0, M, E) relative to MIVQUE remained relatively high (greater than .80) over all parameter sets studied. In practice, this is an upper bound on the efficiency that could be attained for MIVQUE (0, M, E) because estimates for σ_m^2 and σ_e^2 would need to be used in place of the true parameters.

Table 8. Relative efficiency^a of MIVQUE (0, M, E) estimates of (co)variance components relative to MIVQUE estimates computed from mating designs of Thompson^b (1976) and Eisen^b (1967) replicated 200 times each.

Rank ^d	Parameters ^c					Efficiency of				
	$\sigma_m^2 + \sigma_e^2$	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Thompson A Design										
1	79.00	15	15	-.3	20	.99	.99	.99	.99	.99
1	79.00	15	15	-.3	50	.99	.99	.99	.99	.99
3	73.00	15	15	-.1	20	.98	.99	.98	.98	.99
3	73.00	15	15	-.1	50	.99	.99	.99	.99	.99
5	67.72	15	30	-.3	20	.98	.98	.98	.98	.98
5	67.72	15	30	-.3	50	.99	.98	.98	.98	.99
5	67.72	30	15	-.3	20	.97	.98	.98	.98	.97
5	67.72	30	15	-.3	50	.97	.98	.98	.98	.97
9	59.24	15	30	-.1	20	.97	.97	.96	.96	.97
9	59.24	15	30	-.1	50	.99	.98	.98	.97	.99
9	59.24	30	15	-.1	20	.96	.97	.97	.97	.96
9	59.24	30	15	-.1	50	.95	.95	.97	.97	.95
13	58.00	30	30	-.3	20	.96	.98	.97	.97	.96
13	58.00	30	30	-.3	50	.96	.96	.97	.97	.96
15	50.00	27.8	27.8	-.1	46.3	.91	.92	.95	.95	.95
16	46.00	30	30	-.1	20	.95	.96	.96	.95	.91
Thompson B Design										
1	79.00	15	15	-.3	20	.99	.99	.99	.99	.99
1	79.00	15	15	-.3	50	.99	.99	.99	.99	.99
3	73.00	15	15	-.1	20	.98	.99	.99	.99	.98
3	73.00	15	15	-.1	50	.98	.98	.98	.98	.98
5	67.72	15	30	-.3	20	.97	.99	.99	.99	.97
5	67.72	15	30	-.3	50	.98	.98	.98	.97	.98
5	67.72	30	15	-.3	20	.97	.98	.99	.98	.97
5	67.72	30	15	-.3	50	.98	.97	.97	.97	.98
9	59.24	15	30	-.1	20	.96	.98	.99	.97	.96
9	59.24	15	30	-.1	50	.96	.96	.96	.95	.96
9	59.24	30	15	-.1	20	.96	.97	.98	.97	.96
9	59.24	30	15	-.1	50	.96	.94	.93	.94	.96
13	58.00	30	30	-.3	20	.96	.98	.99	.97	.96
13	58.00	30	30	-.3	50	.97	.95	.94	.94	.97
15	50.00	27.8	27.8	-.1	46.3	.95	.92	.90	.91	.95
16	46.00	30	30	-.1	20	.93	.95	.97	.95	.93

Table 8 continued.

Rank ^d	Parameters ^c					Efficiency of				
	$\sigma_m^2 + \sigma_e^2$	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Eisen I Design										
1	79.00	15	15	-.3	20	.95	.96	.95	.95	.96
1	79.00	15	15	-.3	50	.96	.97	.96	.96	.96
3	73.00	15	15	-.1	20	.93	.95	.93	.93	.95
3	73.00	15	15	-.1	50	.94	.96	.94	.95	.95
5	67.72	15	30	-.3	20	.91	.92	.89	.89	.92
5	67.72	15	30	-.3	50	.92	.94	.91	.91	.92
5	67.72	30	15	-.3	20	.90	.93	.91	.92	.92
5	67.72	30	15	-.3	50	.92	.95	.93	.94	.92
9	59.24	15	30	-.1	20	.87	.90	.85	.86	.89
9	59.24	15	30	-.1	50	.91	.94	.90	.89	.90
9	59.24	30	15	-.1	20	.87	.91	.87	.89	.89
9	59.24	30	15	-.1	50	.90	.92	.91	.91	.89
13	58.00	30	30	-.3	20	.88	.89	.86	.87	.88
13	58.00	30	30	-.3	50	.91	.93	.91	.89	.90
15	50.00	27.8	27.8	-.1	46.3	.88	.90	.88	.86	.87
16	46.00	30	30	-.1	20	.81	.85	.81	.81	.82
Eisen II Design										
1	79.00	15	15	-.3	20	.97	.98	.97	.96	.98
1	79.00	15	15	-.3	50	.97	.98	.98	.98	.98
3	73.00	15	15	-.1	20	.95	.97	.96	.95	.96
3	73.00	15	15	-.1	50	.96	.98	.97	.97	.96
5	67.72	15	30	-.3	20	.93	.94	.93	.92	.95
5	67.72	15	30	-.3	50	.94	.96	.96	.96	.95
5	67.72	30	15	-.3	20	.94	.96	.94	.93	.95
5	67.72	30	15	-.3	50	.94	.96	.96	.95	.94
9	59.24	15	30	-.1	20	.89	.93	.91	.91	.91
9	59.24	15	30	-.1	50	.92	.95	.96	.95	.93
9	59.24	30	15	-.1	20	.90	.94	.93	.91	.92
9	59.24	30	15	-.1	50	.90	.93	.93	.93	.90
13	58.00	30	30	-.3	20	.91	.93	.91	.90	.92
13	58.00	30	30	-.3	50	.91	.93	.94	.93	.91
15	50.00	27.8	27.8	-.1	46.3	.88	.90	.92	.91	.88
16	46.00	30	30	-.1	20	.85	.90	.90	.88	.87

Table 8 continued.

Rank ^d	Parameters ^c					Efficiency of				
	$\sigma_m^2 + \sigma_e^2$	σ_g^2	σ_{gm}^2	r_{ggm}	σ_m^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Eisen III Design										
1	79.00	15	15	-.3	20	.98	.98	.98	.97	.98
1	79.00	15	15	-.3	50	.98	.98	.99	.98	.98
3	73.00	15	15	-.1	20	.96	.98	.97	.96	.96
3	73.00	15	15	-.1	50	.97	.98	.98	.98	.97
5	67.72	15	30	-.3	20	.95	.96	.94	.94	.94
5	67.72	15	30	-.3	50	.96	.96	.96	.97	.97
5	67.72	30	15	-.3	20	.95	.97	.96	.95	.95
5	67.72	30	15	-.3	50	.95	.96	.97	.96	.95
9	59.24	15	30	-.1	20	.93	.95	.93	.93	.92
9	59.24	15	30	-.1	50	.94	.96	.96	.96	.94
9	59.24	30	15	-.1	20	.93	.95	.95	.93	.92
9	59.24	30	15	-.1	50	.91	.92	.94	.93	.92
13	58.00	30	30	-.3	20	.93	.94	.93	.92	.93
13	58.00	30	30	-.3	50	.92	.94	.96	.94	.93
15	50.00	27.8	27.8	-.1	46.3	.88	.88	.90	.90	.88
16	46.00	30	30	-.1	20	.89	.92	.91	.90	.89

^a Relative efficiency is the standard error of the MIVQUE estimate of (co)variance component divided by the standard error of the MIVQUE (0, M, E) estimate.

^b Thompson and Eisen Mating designs are defined in the text.

^c Parameters are defined as follows: σ_g^2 , σ_{gm}^2 , σ_m^2 , and σ_e^2 are variances due to direct additive genetic, maternal additive genetic, permanent maternal environmental, and residual error effects; and r_{ggm} and σ_{ggm} are the correlation and covariance between direct and maternal additive genetic effects.

^d Parameter sets are ranked by $\sigma_e^2 + \sigma_m^2$, from high to low.

The efficiencies of MIVQUE(1) estimates of (co)variance components relative to MIVQUE are presented in table 9. Like MIVQUE (0, M, E), the efficiency of MIVQUE(1) relative to MIVQUE remained relatively high (greater than .8) over all parameter sets studied. The efficiencies of MIVQUE (0, M, E) and MIVQUE(1) are similar with MIVQUE (0, M, E) being higher for some parameter sets and MIVQUE(1) being higher for others.

Table 9. The efficiency^a of MIVQUE(1) estimates of (co)variance components relative to MIVQUE estimates computed from 200 sets of designs described by Thompson^b (1976) and Eisen^b (1967).

Parameters ^C					Efficiency of						
σ_g^2	r_{ggm}	σ_{gm}^2	σ_m^2	σ_e^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$		
Thompson A											
15	-.1	15	20	53	.93	.89	.89	.92	.94		
			50	23	.97	.95	.95	.96	.97		
		30	20	39.24	.97	.93	.94	.95	.97		
			50	9.24	.91	.89	.93	.95	.91		
			-.3	15	20	59	.91	.87	.87	.90	.93
	50	29			.97	.94	.94	.95	.97		
	30	20		47.72	.95	.90	.91	.93	.95		
		50		17.72	.95	.92	.94	.95	.95		
		30		-.1	15	20	39.24	.96	.93	.93	.94
	50		9.24			.96	.95	.96	.96	.96	
30	20		26	.99	.97	.97	.97	.99			
	27.8		-.1	27.8	46.3	3.70	.92	.91	.95	.96	.91
					30	-.3	15	20	47.72	.94	.90
50		17.72	.98	.95				.96	.96	.97	
30		20	38	.97		.93	.93	.94	.97		
		50	8	.94	.92	.95	.96	.94			
	Thompson B										
15	-.1	15	20	53	.90	.95	.95	.95	.90		
			50	23	.93	.92	.92	.93	.92		
		30	20	39.24	.94	.96	.95	.96	.94		
			50	9.24	.96	.93	.88	.93	.96		
			-.3	15	20	59	.87	.95	.94	.94	.89
	50	29			.91	.92	.91	.92	.90		
	30	20		47.72	.91	.95	.94	.94	.91		
		50		17.72	.94	.92	.89	.92	.93		
		30		-.1	15	20	39.24	.93	.97	.97	.97
	50		9.24			.95	.94	.92	.94	.95	
30	20		26	.96	.97	.97	.97	.96			
	27.8		-.1	27.8	46.3	3.70	.97	.94	.91	.95	.97
					30	-.3	15	20	47.72	.90	.95
50		17.72	.92	.93				.93	.93	.92	
30		20	38	.93		.96	.95	.96	.96	.92	
		50	8	.95	.92	.90	.93	.94			

Table 9 continued.

Parameters ^C					Efficiency of					
σ_g^2	r_{ggm}	σ_{gm}^2	σ_m^2	σ_e^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$	
Eisen I										
15	-.1	15	20	53	.84	.91	.88	.89	.87	
			50	23	.91	.90	.84	.89	.90	
			30	20	39.24	.91	.93	.90	.93	.91
			50	9.24	.88	.80	.80	.89	.85	
	-.3	15	20	59	.81	.89	.85	.86	.85	
			50	29	.89	.90	.82	.87	.88	
			30	20	47.72	.87	.91	.87	.90	.88
			50	17.72	.90	.85	.80	.90	.87	
	-.1	15	20	39.24	.92	.95	.92	.93	.93	
			50	9.24	.91	.89	.86	.91	.89	
			30	20	26	.96	.95	.93	.96	.95
			27.8	27.8	46.3	3.70	.86	.81	.84	.91
-.3	15	20	47.72	.88	.93	.88	.90	.89		
		50	17.72	.92	.90	.84	.90	.90		
		30	20	38	.92	.93	.90	.93	.92	
		50	8	.88	.82	.81	.89	.84		
Eisen II										
15	-.1	15	20	53	.88	.92	.93	.95	.90	
			50	23	.92	.93	.92	.94	.92	
			30	20	39.24	.93	.95	.93	.95	.93
			50	9.24	.88	.85	.89	.92	.86	
	-.3	15	20	59	.85	.91	.91	.94	.88	
			50	29	.90	.93	.91	.93	.90	
			30	20	47.72	.89	.93	.91	.94	.90
			50	17.72	.90	.89	.88	.91	.89	
	-.1	15	20	39.24	.93	.96	.95	.97	.94	
			50	9.24	.91	.92	.94	.96	.90	
			30	20	26	.96	.97	.95	.97	.96
			27.8	27.8	46.3	3.70	.87	.86	.92	.94
-.3	15	20	47.72	.90	.94	.93	.96	.91		
		50	17.72	.92	.93	.93	.95	.91		
		30	20	38	.93	.95	.93	.96	.93	
		50	8	.89	.87	.90	.93	.87		

Table 9 continued.

Parameters ^C					Efficiency of				
σ_g^2	r_{ggm}	σ_{gm}^2	σ_m^2	σ_e^2	$\hat{\sigma}_g^2$	$\hat{\sigma}_{ggm}$	$\hat{\sigma}_{gm}^2$	$\hat{\sigma}_m^2$	$\hat{\sigma}_e^2$
Eisen III									
15	-.1	15	20	53	.88	.94	.90	.93	.90
			50	23	.92	.91	.90	.94	.91
		30	20	39.24	.93	.94	.93	.95	.93
	-.3	15	50	9.24	.88	.82	.86	.92	.87
			20	59	.86	.92	.88	.91	.87
		30	20	47.72	.89	.93	.90	.94	.90
30	-.1	15	50	17.72	.90	.85	.87	.92	.89
			20	39.24	.94	.96	.93	.96	.94
		30	20	9.24	.92	.90	.91	.95	.90
	-.3	15	26	26	.97	.96	.95	.97	.96
			46.3	3.70	.89	.85	.89	.94	.87
		30	20	47.72	.91	.95	.90	.94	.91
27.8	-.3	15	50	17.72	.92	.91	.90	.95	.91
			20	38	.93	.94	.92	.96	.92
		30	50	8	.90	.85	.87	.93	.87

^a Efficiency is the standard error of the MIVQUE estimate of (co)variance component divided by the standard error of the MIVQUE(1) estimate.

^b Thompson and Eisen mating designs are described in the text.

^c Parameter sets are defined as follows: σ_g^2 , σ_{gm}^2 , σ_m^2 , and σ_e^2 are variances due to direct genic, maternal genic, permanent maternal environmental, and residual effects, and r_{ggm} and σ_{ggm} are the correlation and covariance between direct and maternal genic effects.

SUMMARY AND CONCLUSIONS

In populations of farm animals, there are many different kinds of relatives. In general, analysis of variance (ANOVA) type methods are not adequate to estimate (co)variance components from data in which the animal model is needed because of the complex covariance structure among the observations. Minimum variance quadratic unbiased estimates (MIVQUE) (Rao, 1971) and restricted maximum likelihood estimates (REML) (Patterson and Thompson, 1971) have been extended by Henderson (1985a and b) to an animal model which includes both additive and nonadditive genetic effects. With Henderson's (1985a and b) approach, the mixed model equations (MME) and best linear unbiased predictions (BLUP) for genetic merits are obtained as intermediate results.

Quaas and Pollack (1980) described a reduced animal model (RAM) with MME only for parents that have progeny records equivalent to the animal model with MME for all animals when the genetic model is strictly additive. Using RAM instead of the animal model can save a great deal of computer storage when analyzing performance records from some species. Hudson and Kennedy (1985) found that there were 5.6 times as many total animals as there were parents and ancestors that had progeny with records in Ontario record of performance swine data.

REML and MIVQUE under RAM or the animal model are not computationally feasible with 1986 computers when data sets are large. Therefore, under the animal model or RAM with large data sets, methods

more computationally feasible than REML or MIVQUE are needed to obtain estimates of (co)variance components.

Symmetric differences squared (SDS) (Grimes and Harvey, 1980), weighted symmetric differences squared (WSDS) (Christian, 1980), MIVQUE(0) (Rao, 1971), and diagonal MIVQUE (Henderson) are computationally feasible methods of estimating (co)variance components under RAM or the animal model.

Estimates of (co)variance components by symmetric differences squared (SDS) weighted by the inverse of the error variance-covariance matrix among SDS (WSDS) are minimum variance quadratic unbiased estimates (MIVQUE) when all parameters other than the error variance are near zero. Likewise, estimates of (co)variance components by SDS weighted by the inverse of the total variance-covariance matrix among SDS are MIVQUE for the prior parameters chosen.

The algorithm presented in this paper for obtaining WSDS greatly reduces the computations needed to complete the analysis compared to the WSDS methodology described by Christian (1980). The number of multiplication steps required can be further reduced if the relationships between pairs of animals can be classified into a relatively small number (5 to 100) of relationship categories. This algorithm follows the same approach for reducing the number of multiplications required as Christian (1980) used to reduce the number of multiplications needed to complete SDS. However, WSDS requires more multiplication and addition steps to complete than SDS.

Matrices containing coefficients of relationship for additive and nonadditive genetic effects are needed to apply WSDS or MIVQUE(0) to

models in which these effects are important. Relationship matrices for dominance and epistatic effects can be computed from the numerator relationship matrix (**A**) when there is no inbreeding (Henderson, 1985a). Normally, an additive genetic model is assumed as an approximation when there is inbreeding because the nonadditive effects are difficult to interpret under inbreeding (Cockerham, 1954).

For large data sets under the animal model, the numerator relationship matrix (**A**) is too large to half store in computer core if all $n(n+1)/2$ elements are stored. However, **A** can be stored and used by storing only the $p \leq n(n+1)/2$ nonzero elements (Hudson et al., 1982). This process requires the storage of three vectors of order n and two vectors of order p . Hudson et al. (1982) found that only 6 to 22.6% of the $n(n+1)/2$ elements of the upper triangle of **A** were nonzero for five dairy sire populations. The computational steps required to obtain **A** are proportional to n^2 even with the storage saving procedures of Hudson et al. (1982).

The sampling standard errors computed from 200 sets of designs A and B of Thompson (1976) agree with the standard errors obtained by simulation of the same designs by Grimes and Harvey (1980). These results substantiate the validity of the numerical and simulation methods used in these two studies.

WSDS was more efficient than SDS for most of the design-parameter set combinations studied. Because WSDS was less than 75% efficient relative to MIVQUE (parameters known a priori) for many of the design-parameter set combinations studied, there is a need for computationally feasible methods that are more efficient than WSDS.

MIVQUE with all priors set to zero except for the permanent maternal environmental and residual variance, which were set to their true values (MIVQUE(0,M,E)), and MIVQUE with all priors including the error variance set to one (MIVQUE(1)) were greater than 80% efficient relative to MIVQUE for all design-parameter combinations studied, and were greater than 90% efficient for over half of the design-parameter combinations studied. For MIVQUE(0,M,E), the efficiencies obtained in this study are an upper bound because in practice the priors chosen for permanent maternal environmental and residual variances would have to be estimates instead of the true parameters. MIVQUE(0,M,E) is much easier to compute than MIVQUE or MIVQUE(1) because the inverse of the variance-covariance matrix among observations is easy to compute when all parameters except the permanent maternal environmental and residual variances are assumed to be zero. MIVQUE(1) offers no computational advantage over MIVQUE, but it frees the experimenter from the responsibility of assigning prior values.

A method not considered in the current study which offers potential as far as computational feasibility and efficiency relative to MIVQUE is diagonal MIVQUE (Henderson, 1985a). Numerical studies similar to the current one are needed to study the efficiency of diagonal MIVQUE (Henderson, 1985a) relative to MIVQUE under the animal or reduced animal model. Henderson (1984) states that diagonal MIVQUE is more efficient than MIVQUE(0) when the unknown parameters deviate greatly from zero. Diagonal MIVQUE is only slightly more computationally burdensome to complete than MIVQUE(0) under the animal model.

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APPENDIX A

1. Prove $[\text{tr}(\mathbf{V}_i \mathbf{V}_j)] = \mathbf{X}_1' \mathbf{X}_1 + 2\mathbf{X}_2' \mathbf{X}_2$. [49]

Since \mathbf{V}_i and \mathbf{V}_j are symmetric,

$$[\text{tr}(\mathbf{V}_i \mathbf{V}_j)] = \left[\sum_k (v_{kk})_i (v_{kk})_j \right] + 2 \left[\sum_{k=1}^{n-1} \sum_{l=k+1}^n (v_{kl})_i (v_{kl})_j \right],$$

which can be written as the sum of two row-column multiplications as follows:

$$\begin{aligned} [\text{tr}(\mathbf{V}_i \mathbf{V}_j)] &= [(v_{11})_i (v_{22})_i \dots (v_{nn})_i] \begin{vmatrix} (v_{11})_j \\ (v_{22})_j \\ \vdots \\ (v_{nn})_j \end{vmatrix} \\ &\quad + 2 [(v_{12})_i (v_{13})_i \dots (v_{1n})_i (v_{23})_i \dots (v_{n-1,n})_i] \begin{vmatrix} (v_{12})_j \\ (v_{13})_j \\ \vdots \\ (v_{1n})_j \\ (v_{23})_j \\ \vdots \\ (v_{n-1,n})_j \end{vmatrix}, \end{aligned}$$

which after substituting in [14] and [16] is

$$[\text{tr}(\mathbf{V}_i \mathbf{V}_j)] = \mathbf{X}_1' \mathbf{X}_1 + 2\mathbf{X}_2' \mathbf{X}_2, \text{ which proves [49].}$$

2. Prove $[\mathbf{V}_j \mathbf{1}_n] = \mathbf{H}' \mathbf{X}_2 + \mathbf{X}_1$. [50]

$[\mathbf{V}_j \mathbf{1}_n]$ can be expressed in summation notation as:

$$\begin{aligned}
[V_j 1_n] &= \begin{vmatrix} \sum_k (v_{1k})_j \\ \sum_k (v_{2k})_j \\ \vdots \\ \sum_k (v_{nk})_j \end{vmatrix} = \begin{vmatrix} \sum_{k \neq 1} (v_{1k})_j \\ \sum_{k \neq 2} (v_{2k})_j \\ \vdots \\ \sum_{k \neq n} (v_{nk})_j \end{vmatrix} + \begin{vmatrix} (v_{11})_j \\ (v_{22})_j \\ \vdots \\ (v_{nn})_j \end{vmatrix}, \text{ or} \\
&= H' \begin{vmatrix} (v_{12})_j \\ (v_{13})_j \\ \vdots \\ (v_{1n})_j \\ (v_{23})_j \\ \vdots \\ (v_{n-1,n})_j \end{vmatrix} + \begin{vmatrix} (v_{11})_j \\ (v_{22})_j \\ \vdots \\ (v_{nn})_j \end{vmatrix},
\end{aligned}$$

which after substituting in [14] and [16] is

$$[V_j 1_n] = H' X_2 + X_1, \text{ which proves [50].}$$

3. Prove $[1_n' V_j 1_n] = 1_n' X_1 + 2 1_n' X_2$. [51]

The left side of equality [51] can be written

$$[1_n' V_j 1_n] = 1_n' [V_j 1_n],$$

which after substituting [50] in $[V_j 1_n]$ is

$$[1_n' V_j 1_n] = 1_n' H' X_2 + 1_n' X_1,$$

which after substituting the transpose of [9] for $1_n' H'$ is

$$= 1_n' X_1 + 2 1_n' X_2, \text{ which proves [51].}$$

4. Prove $[Y' V_i Y] = X_1' Y_1 + 2 X_2' Y_2$ [59]

The left side of [59] is

$$[Y' V_i Y] = \left[\sum_k (v_{kk})_i Y_k^2 \right] + 2 \left[\sum_{k=1}^{n-1} \sum_{l=k+1}^n (v_{kl})_i Y_k Y_l \right],$$

which can be written as the sum of 2 row column multiplications as follows:

$$\begin{aligned}
[\mathbf{Y}'\mathbf{V}_i\mathbf{Y}] &= [(v_{11})_i(v_{22})_i \dots (v_{nn})_i] \begin{vmatrix} y_1^2 \\ y_2^2 \\ \vdots \\ y_n^2 \end{vmatrix} \\
&\quad + 2[(v_{12})_i(v_{13})_i \dots (v_{1n})_i(v_{23})_i \dots (v_{n-1,n})_i] \begin{vmatrix} y_1y_2 \\ y_1y_3 \\ \vdots \\ y_1y_n \\ y_2y_3 \\ \vdots \\ y_{n-1}y_n \end{vmatrix},
\end{aligned}$$

which after substituting in [5], [6], [14], and [16] is

$$[\mathbf{Y}'\mathbf{V}_i\mathbf{Y}] = \mathbf{X}_1'\mathbf{Y}_1 + 2\mathbf{X}_2'\mathbf{Y}_2, \text{ which proves [59].}$$

5. Prove $\mathbf{Y}\mathbf{Y}'\mathbf{l}_n = \mathbf{H}'\mathbf{Y}_2 + \mathbf{Y}_1$. [60]

The left hand side of [60] is

$$[\mathbf{Y}\mathbf{Y}'\mathbf{l}_n] = \begin{vmatrix} \sum_k y_1y_k \\ \sum_k y_2y_k \\ \vdots \\ \sum_k y_ny_k \end{vmatrix} = \begin{vmatrix} \sum_{k \neq 1} y_1y_k \\ \sum_{k \neq 2} y_2y_k \\ \vdots \\ \sum_{k \neq n} y_ny_k \end{vmatrix} + \begin{vmatrix} y_1^2 \\ y_2^2 \\ \vdots \\ y_n^2 \end{vmatrix}, \text{ or}$$

$$= \mathbf{H}' \begin{bmatrix} Y_1 Y_2 \\ Y_1 Y_3 \\ \vdots \\ Y_1 Y_n \\ Y_2 Y_3 \\ \vdots \\ Y_{n-1} Y_n \end{bmatrix} + \begin{bmatrix} Y_1^2 \\ Y_2^2 \\ \vdots \\ Y_n^2 \end{bmatrix}, \text{ which after}$$

substituting in [5] and [6] is

$$= \mathbf{H}' \mathbf{Y}_2 + \mathbf{Y}_1, \text{ which proves [60].}$$

6. Prove $\mathbf{l}_n' \mathbf{y} \mathbf{y}' \mathbf{l}_n = \mathbf{l}_n' \mathbf{Y}_1 + 2 \mathbf{l}_q' \mathbf{Y}_2$.

[61]

Substitute [60] into [61] for $\mathbf{y} \mathbf{y}' \mathbf{l}_n$ to obtain

$$= \mathbf{l}_n' \mathbf{H}' \mathbf{Y}_2 + \mathbf{l}_n' \mathbf{Y}_1,$$

which after substituting the transpose of [9] for $\mathbf{l}_n' \mathbf{H}$ is

$$= \mathbf{l}_n' \mathbf{Y}_1 + 2 \mathbf{l}_q' \mathbf{Y}_2, \text{ which proves [61].}$$

APPENDIX B

The multiplier coefficients that specify the contribution of σ_g^2 , σ_{ggm} , σ_{gm}^2 , and σ_m^2 to the covariances among the 18 individuals generated by a replicate of Eisen design I are defined in matrix form as V_1 , V_2 , V_3 , and V_4 . These matrices are as follows:

$$V_1 = \frac{1}{16} \begin{matrix} \text{symmetric} \end{matrix} \begin{matrix} 16 & 8 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 4 & 4 & 8 & 8 & 8 & 8 & 4 & 4 \\ & 16 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 8 & 8 & 4 & 4 & 4 & 4 & 8 & 8 \\ & & 16 & 8 & 8 & 8 & 0 & 0 & 0 & 0 & 8 & 4 & 4 & 4 & 0 & 0 & 0 & 0 \\ & & & 16 & 8 & 8 & 0 & 0 & 0 & 0 & 4 & 8 & 4 & 4 & 0 & 0 & 0 & 0 \\ & & & & 16 & 8 & 0 & 0 & 0 & 0 & 4 & 4 & 8 & 4 & 0 & 0 & 0 & 0 \\ & & & & & 16 & 0 & 0 & 0 & 0 & 4 & 4 & 4 & 8 & 0 & 0 & 0 & 0 \\ & & & & & & 16 & 4 & 4 & 4 & 0 & 0 & 0 & 0 & 8 & 2 & 2 & 2 \\ & & & & & & & 16 & 4 & 4 & 0 & 0 & 0 & 0 & 2 & 8 & 2 & 2 \\ & & & & & & & & 16 & 4 & 0 & 0 & 0 & 0 & 2 & 2 & 8 & 2 \\ & & & & & & & & & 16 & 0 & 0 & 0 & 0 & 2 & 2 & 2 & 8 \\ & & & & & & & & & & 16 & 6 & 4 & 4 & 2 & 2 & 4 & 4 \\ & & & & & & & & & & & 16 & 4 & 4 & 2 & 2 & 4 & 4 \\ & & & & & & & & & & & & 16 & 6 & 4 & 4 & 2 & 2 \\ & & & & & & & & & & & & & 16 & 4 & 4 & 2 & 2 \\ & & & & & & & & & & & & & & 16 & 5 & 3 & 3 \\ & & & & & & & & & & & & & & & 16 & 3 & 3 \\ & & & & & & & & & & & & & & & & 16 & 5 \\ & & & & & & & & & & & & & & & & & 16 \end{matrix}$$

$$V_2 = \frac{1}{4} \begin{matrix} \text{symmetric} \end{matrix} \begin{matrix} 4 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ & & 4 & 4 & 4 & 4 & 0 & 0 & 0 & 0 & 5 & 3 & 3 & 3 & 0 & 0 & 0 & 0 \\ & & & 4 & 4 & 4 & 0 & 0 & 0 & 0 & 3 & 5 & 3 & 3 & 0 & 0 & 0 & 0 \\ & & & & 4 & 4 & 0 & 0 & 0 & 0 & 3 & 3 & 5 & 3 & 0 & 0 & 0 & 0 \\ & & & & & 4 & 0 & 0 & 0 & 0 & 3 & 3 & 3 & 5 & 0 & 0 & 0 & 0 \\ & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 5 & 1 & 1 & 1 \\ & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 5 & 1 & 1 \\ & & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 5 & 1 \\ & & & & & & & & & 4 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 5 \\ & & & & & & & & & & 4 & 2 & 2 & 2 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & 4 & 2 & 2 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & 4 & 2 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & 4 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & & 4 & 1 & 1 & 1 \\ & & & & & & & & & & & & & & & 4 & 1 & 1 \\ & & & & & & & & & & & & & & & & 4 & 1 \\ & & & & & & & & & & & & & & & & & 4 \end{matrix}$$

$$V_3 = \frac{1}{4} \begin{array}{c} \begin{array}{cccccccccccccccccccc} 4 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 4 & 4 & 4 & 4 & 0 & 0 & 0 & 0 & 2 & 2 & 2 & 2 & 0 & 0 & 0 & 0 \\ & & & 4 & 4 & 4 & 0 & 0 & 0 & 0 & 2 & 2 & 2 & 2 & 0 & 0 & 0 & 0 \\ & & & & 4 & 4 & 0 & 0 & 0 & 0 & 2 & 2 & 2 & 2 & 0 & 0 & 0 & 0 \\ & & & & & 4 & 0 & 0 & 0 & 0 & 2 & 2 & 2 & 2 & 0 & 0 & 0 & 0 \\ & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 \\ & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 \\ & & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \\ & & & & & & & & & 4 & 2 & 2 & 2 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & 4 & 2 & 2 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & 4 & 2 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & 4 & 1 & 1 & 1 & 1 \\ & & & & & & & & & & & & & & 4 & 1 & 1 & 1 \\ & & & & & & & & & & & & & & & 4 & 1 & 1 \\ & & & & & & & & & & & & & & & & 4 & 1 \\ & & & & & & & & & & & & & & & & & 4 \end{array} \\ \text{symmetric} \end{array} \end{array},$$

and

$$V_4 = \begin{array}{c} \begin{array}{cccccccccccccccccccc} 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & 1 & 0 & 0 & 0 \\ & & & & & & & & & & & & & & 1 & 0 & 0 \\ & & & & & & & & & & & & & & & 1 & 0 \\ & & & & & & & & & & & & & & & & 1 \end{array} \\ \text{symmetric} \end{array}.$$

The multiplier coefficients that specify the contribution of σ_g^2 , σ_{ggm} , σ_{gm}^2 , and σ_m^2 to the covariances among the 18 individuals generated by a replicate of Eisen design II are defined in matrix form as V_1 , V_2 , V_3 , and V_4 . These matrices are as follows:

$$v_1 = \frac{1}{8}$$

8	0	4	4	0	0	0	0	0	0	2	2	4	4	4	4	0	0
8	8	0	0	4	4	0	0	0	0	4	4	2	2	0	0	4	4
		8	4	0	0	0	0	0	0	4	2	2	2	2	0	0	0
			8	0	0	0	0	0	0	2	4	2	2	2	0	0	0
				8	4	0	0	0	0	2	2	4	2	0	0	2	2
					8	0	0	0	0	2	2	2	4	0	0	2	2
						8	4	4	4	0	0	0	0	4	2	2	2
							8	4	4	0	0	0	0	2	4	2	2
								8	4	0	0	0	0	2	2	4	2
									8	0	0	0	0	2	2	2	4
										8	3	2	2	1	1	2	2
											8	2	2	1	1	2	2
												8	3	2	1	1	1
													8	2	2	1	1
														8	3	1	1
															8	1	1
																8	3
																	8

symmetric

$$v_2 = \frac{1}{4}$$

4	0	4	4	0	0	0	0	0	0	3	3	1	1	1	1	0	0
	4	0	0	4	4	0	0	0	0	1	1	3	3	0	0	1	1
		4	4	0	0	0	0	0	0	5	3	1	1	1	1	0	0
			4	0	0	0	0	0	0	3	5	1	1	1	1	0	0
				4	4	0	0	0	0	1	1	5	3	0	0	1	1
					4	0	0	0	0	1	1	3	5	0	0	1	1
						4	4	4	4	0	0	0	0	5	3	3	3
							4	4	4	0	0	0	0	3	5	3	3
								4	4	0	0	0	0	3	3	5	3
									4	0	0	0	0	3	3	3	5
										4	2	2	2	1	1	0	0
											4	2	2	1	1	0	0
												4	2	0	0	1	1
													4	0	0	1	1
														4	2	2	2
															4	2	2
																4	2
																	4

symmetric

$$V_3 = \frac{1}{2} \begin{pmatrix} 2 & 0 & 2 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 2 & 0 & 0 & 2 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 \\ & & 2 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & 2 & 2 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 \\ & & & & & 2 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & 2 & 2 & 2 & 2 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 \\ & & & & & & & 2 & 2 & 2 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 \\ & & & & & & & & 2 & 2 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 \\ & & & & & & & & & 2 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 \\ & & & & & & & & & & 2 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & 2 & 1 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & 2 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & & 2 & 1 & 1 & 1 \\ & & & & & & & & & & & & & & & 2 & 1 & 1 \\ & & & & & & & & & & & & & & & & 2 & 1 \\ & & & & & & & & & & & & & & & & & 2 \end{pmatrix},$$

symmetric

and

$$V_4 = \begin{pmatrix} 1 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 1 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & & 1 & 0 & 0 & 0 \\ & & & & & & & & & & & & & & & 1 & 0 & 0 \\ & & & & & & & & & & & & & & & & 1 & 0 \\ & & & & & & & & & & & & & & & & & 1 \end{pmatrix}.$$

symmetric

The multiplier coefficients that specify the contribution of σ_g^2 , σ_{ggm} , σ_{gm}^2 , and σ_m^2 to the covariances among the 18 individuals generated by a replicate of Eisen design III are defined in matrix form as V_1 , V_2 , V_3 , and V_4 . These matrices are as follows:

$$v_1 = \frac{1}{16}$$

16	0	8	8	0	0	0	0	0	0	4	4	8	8	8	8	0	0
	16	0	0	8	8	0	0	0	0	8	8	4	4	0	0	8	8
		16	8	0	0	0	0	0	0	8	4	4	4	4	4	0	0
			16	0	0	0	0	0	0	4	8	4	4	4	4	0	0
				16	8	0	0	0	0	4	4	8	4	0	0	4	4
					16	0	0	0	0	4	4	4	8	0	0	4	4
						16	4	4	4	0	0	0	0	8	2	2	2
							16	4	4	0	0	0	0	2	8	2	2
								16	4	0	0	0	0	2	2	8	2
									16	0	0	0	0	2	2	2	8
										16	6	4	4	2	2	4	4
											16	4	4	2	2	4	4
												16	6	4	4	2	2
													16	4	4	2	2
														16	4	4	2
															16	5	1
																16	1
																	16

symmetric

$$v_2 = \frac{1}{4}$$

4	0	4	4	0	0	0	0	0	0	3	3	1	1	1	1	0	0
	4	0	0	4	4	0	0	0	0	1	1	3	3	0	0	1	1
		4	4	0	0	0	0	0	0	5	3	1	1	1	1	0	0
			4	0	0	0	0	0	0	3	5	1	1	1	1	0	0
				4	4	0	0	0	0	1	1	5	3	0	0	1	1
					4	0	0	0	0	1	1	3	5	0	0	1	1
						4	0	0	0	0	0	0	0	5	1	1	1
							4	0	0	0	0	0	0	1	5	1	1
								4	0	0	0	0	0	1	1	5	1
									4	0	0	0	0	1	1	1	5
										4	2	2	2	1	1	0	0
											4	2	2	1	1	0	0
												4	2	2	0	0	1
													4	2	0	0	1
														4	0	0	1
															4	1	1
																4	1
																	4

symmetric

$$V_3 = \frac{1}{4} \begin{array}{c} \begin{array}{cccccccccccccccccccc} 4 & 0 & 4 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 4 & 0 & 0 & 4 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 2 & 0 & 0 & 0 & 0 \\ & & 4 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & 4 & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 2 & 0 & 0 & 0 & 0 \\ & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 2 & 0 & 0 & 0 \\ & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 & 0 \\ & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 & 0 & 0 \\ & & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 2 \\ & & & & & & & & & 4 & 2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & 4 & 2 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & 4 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & 4 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & & 4 & 1 & 1 & 1 \\ & & & & & & & & & & & & & & & 4 & 1 & 1 \\ & & & & & & & & & & & & & & & & 4 & 1 \\ & & & & & & & & & & & & & & & & & 4 \end{array} \\ \text{symmetric} \end{array} \end{array} ,$$

and

$$V_4 = \begin{array}{c} \begin{array}{cccccccccccccccccccc} 1 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 1 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & 1 & 0 & 0 & 0 & 0 & 0 \\ & & & & & & & & & & & & & 1 & 0 & 0 & 0 \\ & & & & & & & & & & & & & & 1 & 0 & 0 \\ & & & & & & & & & & & & & & & 1 & 0 \\ & & & & & & & & & & & & & & & & 1 \end{array} \\ \text{symmetric} \end{array} .$$

The multiplier coefficients that specify the contribution of σ_g^2 , σ_{ggm} , σ_{gm}^2 , and σ_m^2 to the covariances among the eight individuals generated by a replicate of Thompson design A are defined in matrix form as V_1 , V_2 , V_3 , and V_4 . These matrices are as follows:

$$\begin{aligned}
 \mathbf{V}_1 &= \frac{1}{16} \begin{vmatrix} 16 & 8 & 4 & 4 & 8 & 8 & 2 & 2 \\ & 16 & 4 & 4 & 4 & 4 & 2 & 2 \\ & & 16 & 8 & 2 & 2 & 4 & 4 \\ & & & 16 & 2 & 2 & 8 & 8 \\ & & & & 16 & 8 & 1 & 1 \\ & \text{symmetric} & & & & 16 & 1 & 1 \\ & & & & & & 16 & 8 \\ & & & & & & & 16 \end{vmatrix}, \\
 \mathbf{V}_2 &= \frac{1}{8} \begin{vmatrix} 8 & 8 & 0 & 0 & 2 & 2 & 2 & 2 \\ & 8 & 0 & 0 & 2 & 2 & 2 & 2 \\ & & 8 & 8 & 0 & 0 & 6 & 6 \\ & & & 8 & 0 & 0 & 10 & 10 \\ & & & & 8 & 8 & 1 & 1 \\ & \text{symmetric} & & & & 8 & 1 & 1 \\ & & & & & & 8 & 8 \\ & & & & & & & 8 \end{vmatrix}, \\
 \mathbf{V}_3 &= \frac{1}{2} \begin{vmatrix} 2 & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 2 & 2 & 0 & 0 & 1 & 1 \\ & & & 2 & 0 & 0 & 1 & 1 \\ & & & & 2 & 2 & 0 & 0 \\ & \text{symmetric} & & & & 2 & 0 & 0 \\ & & & & & & 2 & 2 \\ & & & & & & & 2 \end{vmatrix}, \\
 \mathbf{V}_4 &= \begin{vmatrix} 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 1 & 1 & 0 & 0 & 0 & 0 \\ & & & 1 & 0 & 0 & 0 & 0 \\ & \text{symmetric} & & & 1 & 1 & 0 & 0 \\ & & & & & 1 & 0 & 0 \\ & & & & & & 1 & 1 \\ & & & & & & & 1 \end{vmatrix}.
 \end{aligned}$$

and

$$\mathbf{V}_4 = \begin{vmatrix} 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 1 & 1 & 0 & 0 & 0 & 0 \\ & & & 1 & 0 & 0 & 0 & 0 \\ & \text{symmetric} & & & 1 & 1 & 0 & 0 \\ & & & & & 1 & 0 & 0 \\ & & & & & & 1 & 1 \\ & & & & & & & 1 \end{vmatrix}.$$

The multiplier coefficients that specify the contribution of σ_g^2 , σ_{ggm}^2 , σ_{gm}^2 , and σ_m^2 to the covariances among the eight individuals generated by a replicate of Thompson design B are defined in matrix form as \mathbf{V}_1 , \mathbf{V}_2 , \mathbf{V}_3 , and \mathbf{V}_4 . These matrices are as follows:

$$v_1 = \frac{1}{16} \begin{vmatrix} 16 & 8 & 4 & 4 & 8 & 8 & 2 & 2 \\ & 16 & 4 & 4 & 4 & 4 & 2 & 2 \\ & & 16 & 8 & 2 & 2 & 4 & 4 \\ & & & 16 & 2 & 2 & 8 & 8 \\ & & & & 16 & 8 & 1 & 1 \\ \text{symmetric} & & & & & 16 & 1 & 1 \\ & & & & & & 16 & 8 \\ & & & & & & & 16 \end{vmatrix},$$

$$v_2 = \frac{1}{4} \begin{vmatrix} 4 & 4 & 0 & 0 & 5 & 5 & 1 & 1 \\ & 4 & 0 & 0 & 3 & 3 & 1 & 1 \\ & & 4 & 4 & 1 & 1 & 3 & 3 \\ & & & 4 & 1 & 1 & 5 & 5 \\ & & & & 4 & 4 & 1 & 1 \\ \text{symmetric} & & & & & 4 & 1 & 1 \\ & & & & & & 4 & 4 \\ & & & & & & & 4 \end{vmatrix},$$

$$v_3 = \frac{1}{4} \begin{vmatrix} 4 & 4 & 0 & 0 & 2 & 2 & 0 & 0 \\ & 4 & 0 & 0 & 2 & 2 & 0 & 0 \\ & & 4 & 4 & 0 & 0 & 2 & 2 \\ & & & 4 & 0 & 0 & 2 & 2 \\ & & & & 4 & 4 & 1 & 1 \\ \text{symmetric} & & & & & 4 & 1 & 1 \\ & & & & & & 4 & 4 \\ & & & & & & & 4 \end{vmatrix},$$

and

$$v_4 = \begin{vmatrix} 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & 1 & 1 & 0 & 0 & 0 & 0 \\ & & & 1 & 0 & 0 & 0 & 0 \\ \text{symmetric} & & & & 1 & 1 & 0 & 0 \\ & & & & & 1 & 0 & 0 \\ & & & & & & 1 & 1 \\ & & & & & & & 1 \end{vmatrix}.$$

APPENDIX C

Computational example follows for symmetric differences squared (SDS) and SDS weighted by the inverse of the error variance-covariance matrix among SDS when relationship categories are considered.

Suppose that the observations generated from one replicate of design A of Thompson (1976) are

$$\mathbf{y} = [25 \ 13 \ 37 \ 11 \ 7 \ 4 \ 9 \ 21]' .$$

Assume that $\text{Var}(\mathbf{y})$ is the same as assumed in Appendix B. Hence,

$$\mathbf{1}_n' \mathbf{y} = 127, \text{ and}$$

$$\bar{y} = 15.875 .$$

\mathbf{U} contains the first 4 columns of table 1 of Grimes and Harvey (1980), excluding the 9th row, plus a column of zeros for the fifth column. Hence,

$$\mathbf{U} = (1/16) \begin{vmatrix} 4 & 0 & 0 & 0 & 0 \\ 2 & 0 & 0 & 0 & 0 \\ 8 & 16 & 16 & 16 & 0 \\ 8 & 20 & 8 & 0 & 0 \\ 8 & 4 & 0 & 0 & 0 \\ 4 & 12 & 8 & 0 & 0 \\ 2 & 4 & 0 & 0 & 0 \\ 4 & 4 & 0 & 0 & 0 \\ 1 & 2 & 0 & 0 & 0 \end{vmatrix} .$$

\mathbf{Q} is obtained from the 5th column of table 1 of Grimes and Harvey (1980), excluding the 9th row. Hence,

$$\mathbf{Q} = [4 \ 4 \ 4 \ 2 \ 2 \ 2 \ 4 \ 2 \ 4]' .$$

The 4 in the first element of \mathbf{Q} , means that there are four pairs of individuals in a set of this design related as paternal half-sibs. \mathbf{N}

is obtained from figure 1 and table 1 of Grimes and Harvey (1980).

Hence,

$$N' = \begin{vmatrix} 2 & 2 & 2 & 2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 2 & 2 & 2 & 2 & 0 & 0 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 0 & 0 & 0 & 2 & 0 & 0 & 1 & 1 \\ 2 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 2 & 0 & 0 & 0 & 1 & 1 \\ 2 & 2 & 0 & 0 & 0 & 0 & 2 & 2 \\ 0 & 2 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 2 & 2 & 2 & 2 \end{vmatrix} .$$

A 2 in the first row and column of N' , means that there are two animals related to P_1 as paternal half-sibs. Therefore,

$$N'N = \begin{vmatrix} 16 & 8 & 8 & 4 & 4 & 4 & 8 & 4 & 0 \\ & 16 & 8 & 4 & 4 & 4 & 0 & 4 & 8 \\ & & 8 & 4 & 4 & 4 & 8 & 4 & 8 \\ & & & 6 & 0 & 2 & 4 & 0 & 4 \\ & & & & 6 & 0 & 4 & 2 & 4 \\ & \text{symmetric} & & & & 6 & 4 & 0 & 4 \\ & & & & & & 16 & 4 & 8 \\ & & & & & & & 6 & 4 \\ & & & & & & & & 16 \end{vmatrix} .$$

The vectors of squares (Y_1) and crossproducts (Y_2) among observations (y) are

$$Y_1 = [625 \ 169 \ 1369 \ 121 \ 49 \ 16 \ 81 \ 441]' , \text{ and}$$

$$Y_2 = [325 \ 925 \ 275 \ 175 \ 100 \ 225 \ 525 \ 481 \ 143 \ 91 \ 52 \ 117 \ 273 \ 407 \\ 259 \ 148 \ 333 \ 777 \ 77 \ 44 \ 99 \ 231 \ 28 \ 63 \ 147 \ 36 \ 84 \ 189]' .$$

We can let

$$B = \text{Diag}(Q)$$

The incidence matrix that specifies the relationship category to which the elements of Y_2 belong is

$$Z = \begin{bmatrix} 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} .$$

Z does not need to be stored, but is given here for completeness.

Therefore,

$$Z'Y_2 = [1824 \ 528 \ 949 \ 330 \ 275 \ 1110 \ 1140 \ 143 \ 330]' .$$

Applying equations [89] and [90],

$$X'W^{-1}X = \begin{bmatrix} 5.23828 & 6.10156 & 6.46875 & 6.375 & 5.1875 \\ & 11.0781 & 10.1875 & 8.75 & 4.375 \\ & & 11.25 & 11 & 5.5 \\ \text{symmetric} & & & 12 & 6 \\ & & & & 7 \end{bmatrix} ,$$

and

$$X'W^{-1}Y = [594.633 \ 641.391 \ 708.313 \ 736.75 \ 854.875]' .$$

Therefore,

$$(X'W^{-1}X)^{-1}X'W^{-1}Y = [-195.7 \quad 148.6 \quad -142.9 \quad 72.3 \quad 219.5]' ,$$

which are the WSDS estimates of the variance due to direct genic effects, the covariance between direct and maternal genic effects, the variance due to maternal genic effects, the variance due to permanent maternal environmental effects, and the variance due to residual effects. Applying equations [91] and [92],

$$X'X = \begin{vmatrix} 64.5625 & 57.6250 & 70 & 75 & 83 \\ & 63.2500 & 70 & 70 & 70 \\ & & 84 & 88 & 88 \\ \text{symmetric} & & & 96 & 96 \\ & & & & 112 \end{vmatrix} ,$$

and

$$X'Y = [10131.8 \quad 9166.5 \quad 10588 \quad 11732 \quad 13678]' .$$

Therefore,

$$(X'X)^{-1}X'Y = [-232.3 \quad 538.6 \quad -905.4 \quad 503.1 \quad 237.8]' ,$$

which are the SDS estimates of the variance due to direct genic effects, the covariance between direct and maternal genic effects, the variance due to maternal genic effects, the variance due to permanent maternal environmental effects, and variance due to residual effects.

Note for this example that the number of relationship categories was 9 for only 8 animals. Normally in practice the number of relationship categories would be quite small (less than 50) and the number of animals could be in the thousands. Note that two estimates of variance components are negative. This can happen with high probability for an example this small.